

A REVISION OF THE NEARCTIC GENUS *GYMNOCARENA* HERING
(DIPTERA: TEPHRITIDAE)

ALLEN L. NORRBOM

Systematic Entomology Laboratory, USDA, ARS, PSI, % National Museum of Natural History, NHB 168, Washington, D.C. 20560.

Abstract.—The genus *Gymnocarena* Hering is revised to include 13 Nearctic species: *angusta*, n. sp., *apicata* (Thomas), n. comb., *bicolor* Foote, *carinata*, n. sp., *diffusa* (Snow), *fusca*, n. sp., *hernandezi*, n. sp., *lichtensteinii* (Wiedemann), n. comb., *magna*, n. sp., *mexicana* (Aezél), *mississippiensis*, n. sp., *serrata*, n. sp., and *tricolor* (Doane). *Mylogymnocarena* Foote is a new synonym of *Gymnocarena*, and *flava* Foote is a new synonym of *tricolor*. A lectotype is designated for *lichtensteinii*. New host data are presented for *carinata* and *mexicana*, and it is noted that all known hosts of *Gymnocarena* belong to the tribe Heliantheae (Asteraceae). Cladistic relationships among the species are analyzed, and descriptions, illustrations, and distribution maps for all species, as well as a key, are provided.

Resumen.—El género *Gymnocarena* Hering se revisa para incluir 13 especies nearcticas: *angusta*, sp. n., *apicata* (Thomas), comb. n., *bicolor* Foote, *carinata*, sp. n., *diffusa* (Snow), *fusca*, sp. n., *hernandezi*, sp. n., *lichtensteinii* (Wiedemann), comb. n., *magna*, sp. n., *mexicana* (Aezél), *mississippiensis*, sp. n., *serrata*, sp. n., and *tricolor* (Doane). *Mylogymnocarena* Foote es un sinonimo nuevo de *Gymnocarena*, y *flava* Foote es un sinonimo nuevo de *tricolor*. Un lectotipo se designa para *lichtensteinii*. Datos huéspedes nuevos se presentan para *carinata* y *mexicana*, y se reporta que todos huéspedes conocidos de *Gymnocarena* pertenecen al tribu Heliantheae (Asteraceae). Relaciones cladísticas entre las especies se analizan, y descripciones, ilustraciones, mapas de distribución por todos las especies, y una clave, se proveen.

Key Words: Fruit flies, *Helianthus*, *Dahlia*, *Verbesina*, taxonomy

The genus *Gymnocarena* Hering includes 13 species, seven of which are newly described in this paper. They are relatively large fruit flies, 4.0–7.5 mm long, with wing patterns of solid brown and/or yellow with large hyaline or whitish marks. *Gymnocarena* is endemic to North America, occurring from the central and western United States and Canada to central Mexico. Host data are limited, but the species whose biologies are known breed in flower heads of plants in the tribe Heliantheae of the Asteraceae.

The type species, *G. diffusa* (Snow), is sometimes a pest of commercial sunflowers.

MATERIALS AND METHODS

Acronyms for the depositories of specimens listed in the text are as follows: ANSP—Academy of Natural Sciences; AMNH—American Museum of Natural History; BMNH—Natural History Museum (formerly British Museum); CAS—California Academy of Sciences; CDA—California Department of Agriculture; CNC—

Canadian National Collection; CSUFC—Colorado State University; FLBPC—F. L. Blanc personal collection; FMNH—Field Museum of Natural History; FSCA—Florida State Collection of Arthropods; JJPC—J. Jenkins personal collection; INHS—Illinois Natural History Survey; KSU—Kansas State University; MCZ—Museum of Comparative Zoology, Harvard University; MSUEL—Michigan State University; NMW—Naturhistorisches Museum Wien; SDNHM—San Diego Natural History Museum; TAMU—Texas A&M University; UAE—University of Alberta, Edmonton; UAT—University of Arizona; UCB—University of California, Berkeley; UCR—University of California, Riverside; UKaL—Snow Entomological Museum, University of Kansas; UMMZ—University of Michigan, Museum of Zoology; UNAM—Instituto de Biología, Universidad Nacional Autónoma de México; UNL—University of Nebraska; USNM—National Museum of Natural History, Smithsonian Institution; USU—Utah State University; WSU—Washington State University; ZMHU—Zoologisches Museum der Humboldt Universität.

I follow the morphological terminology of McAlpine (1981), except as noted in Norrbom and Kim (1988). The length of female syntergosternite 7 was measured dorsally, to the ridge at the base, and does not include the apodemes. The size and shape of the facial carina is a useful character in *Gymnocarena*, although it varies subtly among some species. Its size refers in this paper to how much it is produced from the plane of the face. The height of the ventral, laterally expanded part was measured in comparison to that of the face, which was measured to the ventral margin of the antennal sockets. Within the light areas of the wing in most species there are distinctive patterns of white spots within slightly darker grayish or light brown areas. These patterns, apparently due to microtrichia color, may be difficult to see, especially

in teneral specimens. The term "light" is used in this paper to refer collectively to hyaline, white, or grayish areas, as they are often difficult to differentiate.

RELATIONSHIPS

Norrbom (1987) transferred *Gymnocarena* to the subfamily Tephritinae because it does not have distinctly differentiated scapular setae and because of its Asteraceae hosts. Further supporting this hypothesis is the shape of the epandrium and outer surstyli, which is almost oval (Fig. 1C, E), with the margin of the surstylus usually projected to form a dorsal lobe (Fig. 1B, D). This shape is common within the Tephritinae and may be the groundplan condition for the subfamily. It does not occur in the Trypetinae.

Within the Tephritinae, the relationship of *Gymnocarena* is unclear. It shares a number of plesiomorphic character states with the Terelliini and a group of mainly neotropical genera including *Acrotaenia* and *Polionota* (see Norrbom 1987), but I have discovered no synapomorphies indicating its relationship to any other taxon. The following are character states of *Gymnocarena* that are probably plesiomorphic for the Tephritinae: frons non-setulose medially; postocular setae and scutal setulae slender to slightly swollen; 3 or more pairs of frontal setae; dorsocentral seta usually more or less aligned with postsutural supra-alar seta; vein R_1 without gap in dorsal setulae near apex of vein *sc*; vein R_{4+5} setose dorsally to beyond *dm-cu*; cell *bcu* with apical lobe large, one-third to one-half width of cell.

The monophyly of *Gymnocarena* is indicated by a synapomorphy of the male genitalia—the distiphallus has spines on the membranous apical part (Fig. 1A). This type of distiphallus is unique within the Tephritidae to my knowledge. The lack of microtrichia on most of the arista except basally (Fig. 2) may also be a synapomorphy. In most Tephritinae there are at least minute microtrichia. In addition, most other characters that are important at the generic level

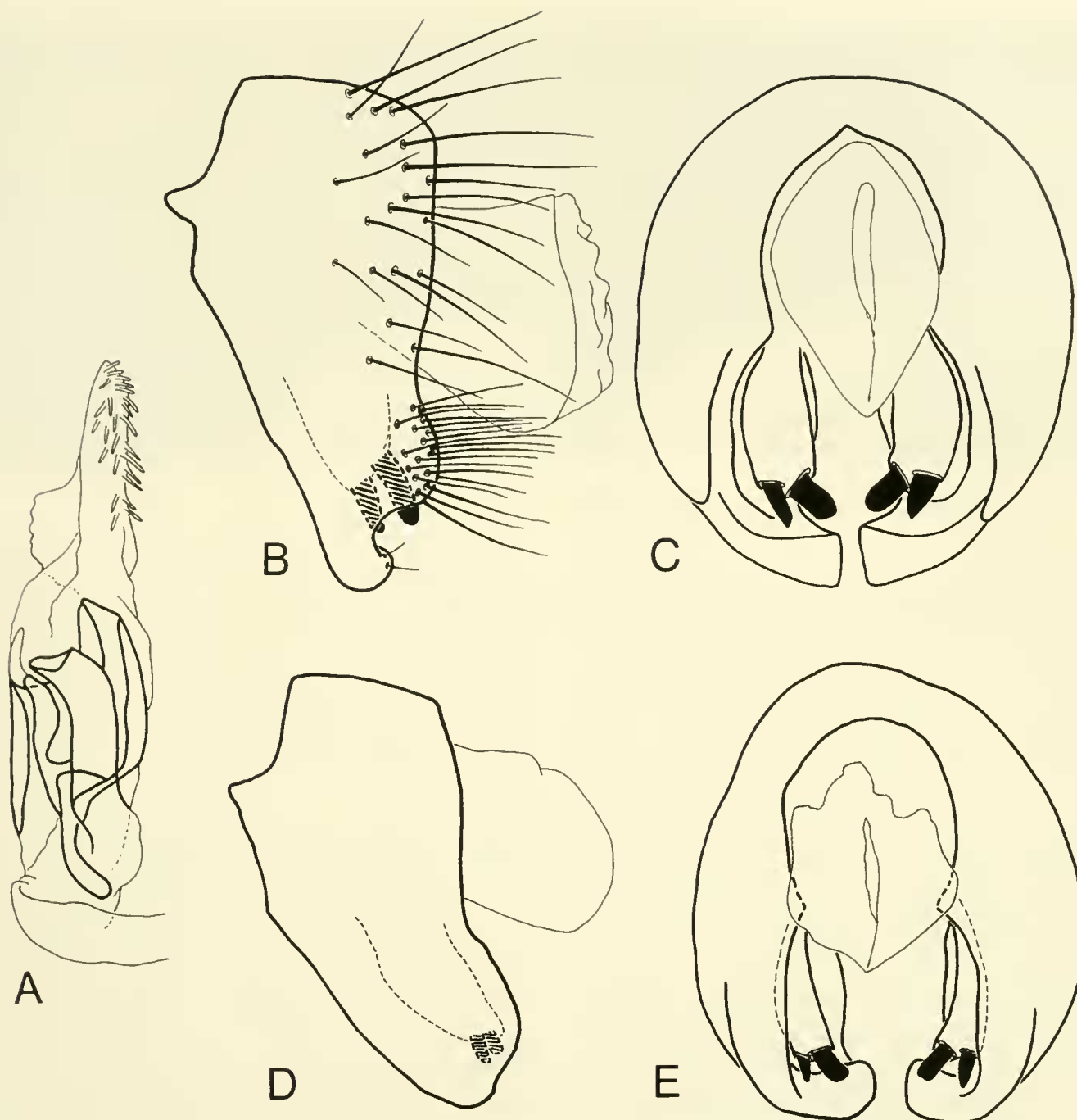


Fig. 1. Male terminalia: A–C, *diffusa* (Snow); D–E, *mexicana* (Aczél); A, distiphallus; B, D, epandrium and outer surstyli, lateral view; C, E, same, posterior view.

in the Tephritidae, such as chaetotaxy, head shape, outer surstylus shape, and wing venation, are consistent within *Gymnocarena*. Some of these characters could also be apomorphies for the genus, but cannot be evaluated because its sister group is unknown. Their consistency at least does not contradict a hypothesis of monophyly.

As delimited here, *Gymnocarena* includes the genera *Tomoplagiodes* Aczél and *Mylogymnocarena* Foote. The latter is a new synonym. Blanc and Foote (1987) recog-

nized its similarity with *Gymnocarena* and admitted that it may be congeneric, but they proposed several characters to separate the two taxa. When other characters and the new species described in this paper are considered, however, this classification does not seem valid. Of the characters used by Blanc and Foote, I found the angle between the crossveins to be highly variable intraspecifically when I examined larger series of specimens. The swollen femora appear to be an apomorphic character state of *diffusa*

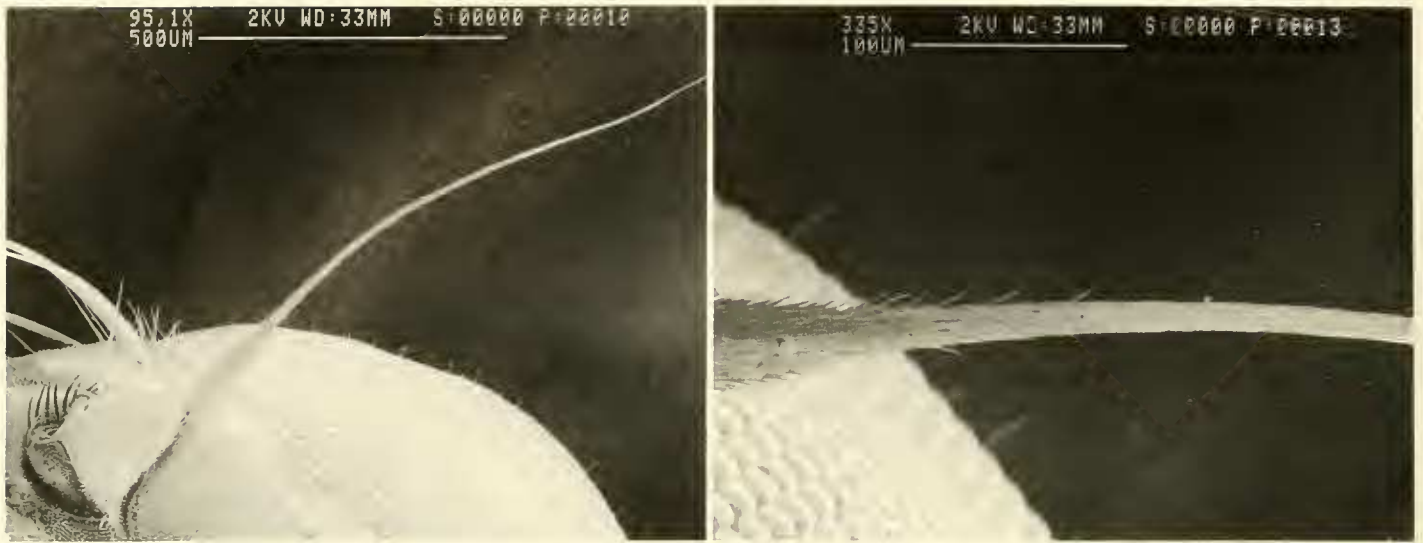


Fig. 2. Antenna of *mexicana*: A, arista; B, base of arista, enlarged.

and *tricolor*, but wing pattern color, the number of hyaline areas in cell r_1 , and a number of other characters (see Tables 1 and 2) exhibit considerable homoplasy and do not consistently divide the species into distinct subgroups. I see no reason, therefore, to continue to recognize *Mylogymnocarena*.

Relationships within *Gymnocarena* are poorly resolved. I was able to recognize only 7 characters that are useful for cladistic analysis of the included species. These and their states are listed in Tables 1 and 2. Other characters that are somewhat useful taxonomically, such as genal height and syntergosternite 7 length, are so variable that I was unable to interpret them for phylogenetic analysis. Another potentially useful character, the size of the dorsal lobe of the outer surstylus, is unknown for too many taxa. The diverse wing patterns of *Gymnocarena* contain considerable phylogenetic information, but they are very difficult to divide into states and to order into transformation series. I tried dividing the pattern into several characters based on certain areas of the wing, but as this seemed to result in additional homoplasy in early analyses, I eventually recognized just one character (i.e. general wing pattern) with five states.

The characters were analyzed using Hennig86 (J. S. Farris, copyrighted; see Far-

ris 1988, Fitzhugh 1989). The implicit enumeration option (ie*) was used in all runs. Determination of character polarity was hindered by the fact that the sister group of *Gymnocarena* is unknown. For most characters, one state is found in most or all other Tephritinae, and this state was considered plesiomorphic and was assigned to the hypothetical outgroup used in the analysis. This was not possible for characters 2 and 5, as the abdominal setulae color and wing pattern vary considerably in other Tephritinae. For these characters, I ran several analyses varying the states assigned to the outgroup. Only states 1 and 2 were used for character 2, as I guessed these to be the more likely plesiomorphic states. Nonredundant coding (O'Grady and Deets 1987) was used to transform character 2 for analysis by Hennig86 which does not accept nonlinear multistate characters. The types of *G. carinata* were reared after this paper was submitted for publication and after the illustrations of the phylogenetic hypotheses had been prepared. This species is not included in the analysis, although it has the same character states as *G. serrata* and *fusca*, and appears to be most closely related to them.

Some examples of trees resulting from the analyses are shown in Figs. 3–4, but there are many other trees of equal length that represent equally parsimonious hypotheses

Table 1. Characters and states used in phylogenetic analysis of *Gymnocarena*. Unless otherwise noted, state 0 is hypothesized as plesiomorphic.

1. Femora—0) not swollen; 1) swollen.
2. Wing pattern—0) highly reduced, not dark basal to dm-cu, but dark area with light spots; 1) extensive, with many light spots, yellow at least basally, light area in radial cells small and distinctly divided; 2) extensive, with few light spots, dark areas entirely brown, light area in radial cells large and partially divided; 3) extensive, with few light spots, dark areas entirely brown, light area in radial cells small and undivided or absent; 4) reduced, dark areas entirely brown, light area in radial cells large, only partially or not divided. This character is hypothesized as a linear transformation series, except that states 3 and 4 are considered independently derived from state 2. The plesiomorphic state is also uncertain, although states 1 or 2 seem most likely.
3. Facial carina size—0) weakly to moderately developed; 1) moderately to well developed.
4. Cuticle—0) never with tiny dark spots; 1) with tiny dark spots in at least some specimens.
5. Abdominal setulae—0) brownish except on syntergite 1+2; 1) entirely yellowish. The polarity of this character is uncertain.
6. Aculeus tip shape—0) moderately broad, strongly tapered; 1) very slender basally and apically; 2) broad apically. States 1 and 2 are hypothesized as independently derived from state 0.
7. Aculeus tip margin—0) non-serrate; 1) serrate.

of the relationships among the species of *Gymnocarena*. The only consistent results of all of the analyses are the following groups of species: *diffusa* + *tricolor*; *serrata* + *fusca*; and *magna* + *lichtensteinii* + *mexicana*. The first pair is the most strongly supported clade, with 2–4 synapomorphies. These always include character 1 (swollen femora), but the others vary, depending upon the hypotheses of polarity used in the analyses (e.g. state 1 of character 5 is a synapomorphy if state 0 is assigned to the outgroup; or, in trees where *diffusa* + *tricolor* is not the basal clade, character 4, state 1 (cuticle with tiny dark spots) occurs as a synapomorphy for the genus, with the reversal to state 0 (cuticle without spots) a synapomorphy for *diffusa* and *tricolor* (see Fig. 4)). The *serrata* + *fusca*

Table 2. Character state distributions in species of *Gymnocarena* and four hypothetical outgroups.

Character No.	1234567
hypoth. outgr. A	0100100
hypoth. outgr. B	0200100
hypoth. outgr. C	0100000
hypoth. outgr. D	0200000
<i>diffusa</i>	1110120
<i>tricolor</i>	1110120
<i>bicolor</i>	0301020
<i>hernandezi</i>	0311020
<i>magna</i>	0411020
<i>lichtensteinii</i>	04110??
<i>mexicana</i>	0411020
<i>angusta</i>	0211010
<i>apicata</i>	0001010
<i>mississippiensis</i>	0101010
<i>serrata</i>	0301001
<i>fusca</i>	0301001

clade is supported by a unique synapomorphy in character 7 (aculeus tip serrate), and *magna* + *lichtensteinii* + *mexicana* are grouped consistently by character 2, state 4 (wing pattern reduced). Another common clade is *apicata* + *mississippiensis*, which is frequently the sister group to *angusta*. These 3 species are grouped by character 6, state 1 (aculeus slender), but *angusta* often runs elsewhere because of differences in characters 2 (wing pattern) and 3 (facial carina size). Usually, *bicolor* and *hernandezi* are found in clades including *serrata* + *fusca* and/or *magna* + *lichtensteinii* + *mexicana*.

The polarity of character 5 (abdominal setulae color) has considerable effect on the analyses. When the hypothetical outgroup is assigned state 1 for this character (i.e. state 1 plesiomorphic), the usual results are trees with *diffusa* + *tricolor* as the sister group of the remaining species. With this polarity, state 0 of character 5 and state 1 of character 4 are synapomorphies for the remaining species. With this polarity for character 5 and with state 1 in the outgroup for character 2 (Table 2, outgroup A), 14 trees of length 16 (ci = 68, ri = 81) result, all with *diffusa* + *tricolor* as the basal clade. Two of

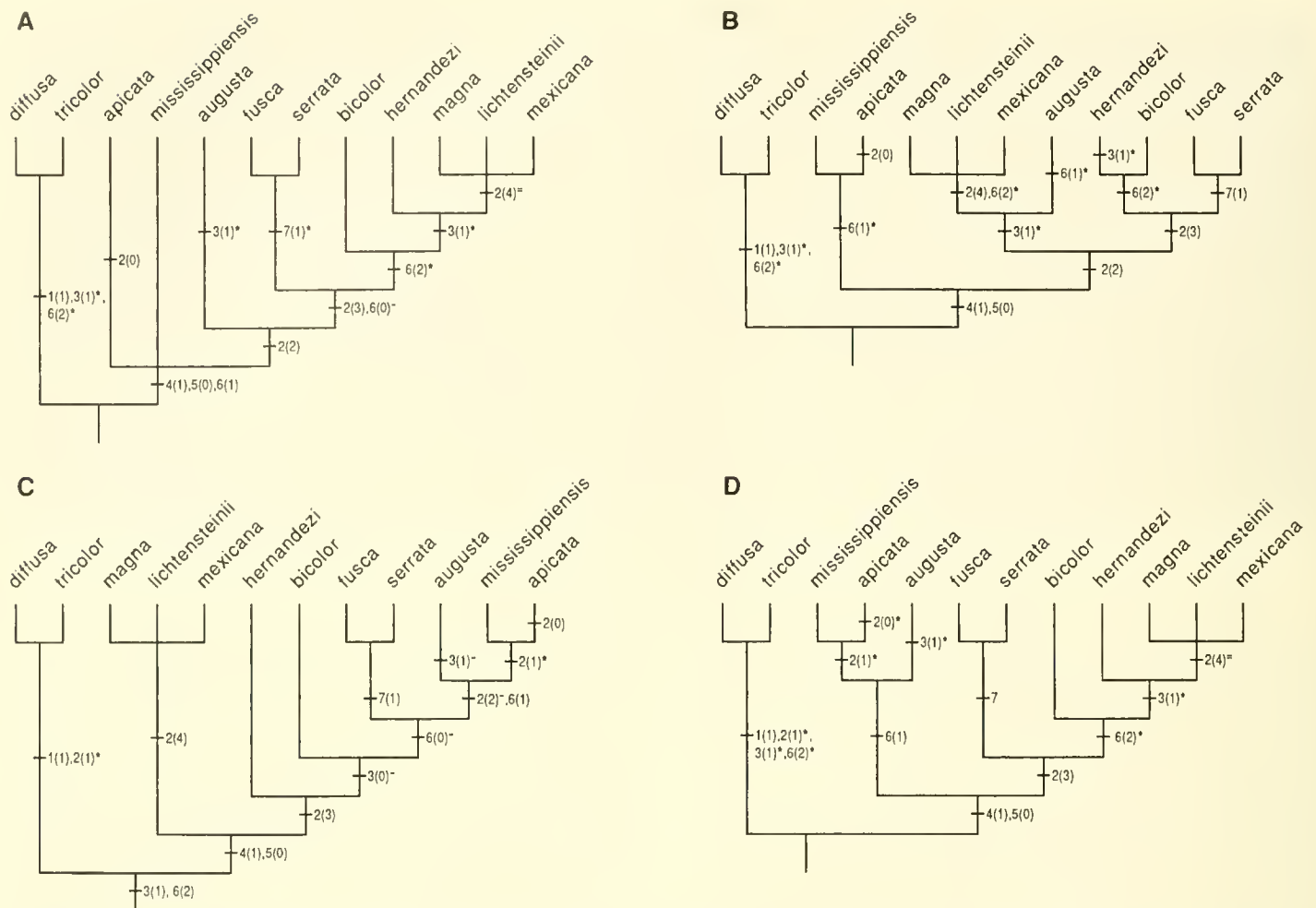


Fig. 3. Examples of hypotheses of phylogenetic relationships among the species of *Gymnocarena* if state 1 of character 5 is assigned to outgroup. A, B, 2 of 16 trees resulting if state 1 is assigned for character 2 (Table 2, outgroup A); C, D, 2 of 5 trees resulting if state 2 is assigned for character 2 (Table 2, outgroup B). Numbers refer to characters, those in parentheses to states, listed in tables 1 and 2. "*" indicates homoplasy, "-" indicates reversal.

these are shown in Fig. 3A–B. With state 2 in the outgroup for character 2 (Table 2, outgroup B), 5 trees of length 16 ($ci = 68$, $ri = 80$) result, in 4 of which *diffusa* + *tricolor* is the basal clade (e.g. Fig. 3C–D). The remaining tree has the same topology as Fig. 4A, with *apicata* + *mississippiensis* + *angusta* as the basal lineage, and with *diffusa* + *tricolor* closest to *magna* + *lichtensteinii* + *mexicana*. It differs from the tree of Fig. 4A only in having an additional step at the base because character 5 state 1 was assigned to the outgroup.

Assigning state 0 to the outgroup for character 5 changes the tree morphology considerably. With state 1 in the outgroup for character 2 (Table 2, outgroup C) the results are ambiguous; 30 trees of length 16 ($ci = 68$, $ri = 80$) result, some with *diffusa* + *tricolor* the basal clade (e.g. Fig. 4B), some

with *apicata* + *mississippiensis* (sometimes also + *angusta*) as the basal lineage (e.g. Fig. 4C), and some with a basal trichotomy of *apicata*, *mississippiensis*, and the remaining species (e.g. Fig. 4D). With state 2 in the outgroup for character 2 (Table 2, outgroup D), only 1 tree results, of length 15 ($ci = 73$, $ri = 84$). In this tree (Fig. 4A), *apicata* + *mississippiensis* + *angusta* are the sister group to the remaining species. The latter interpretation of polarities may be slightly preferable over the others given the slightly shorter length and higher consistency and retention indices of the tree.

HOST DATA

Species of *Helianthus*, *Verbesina*, and *Dahlia* are the only confirmed host plants of *Gymnocarena*. All three plant genera belong to the tribe Heliantheae of the Aster-

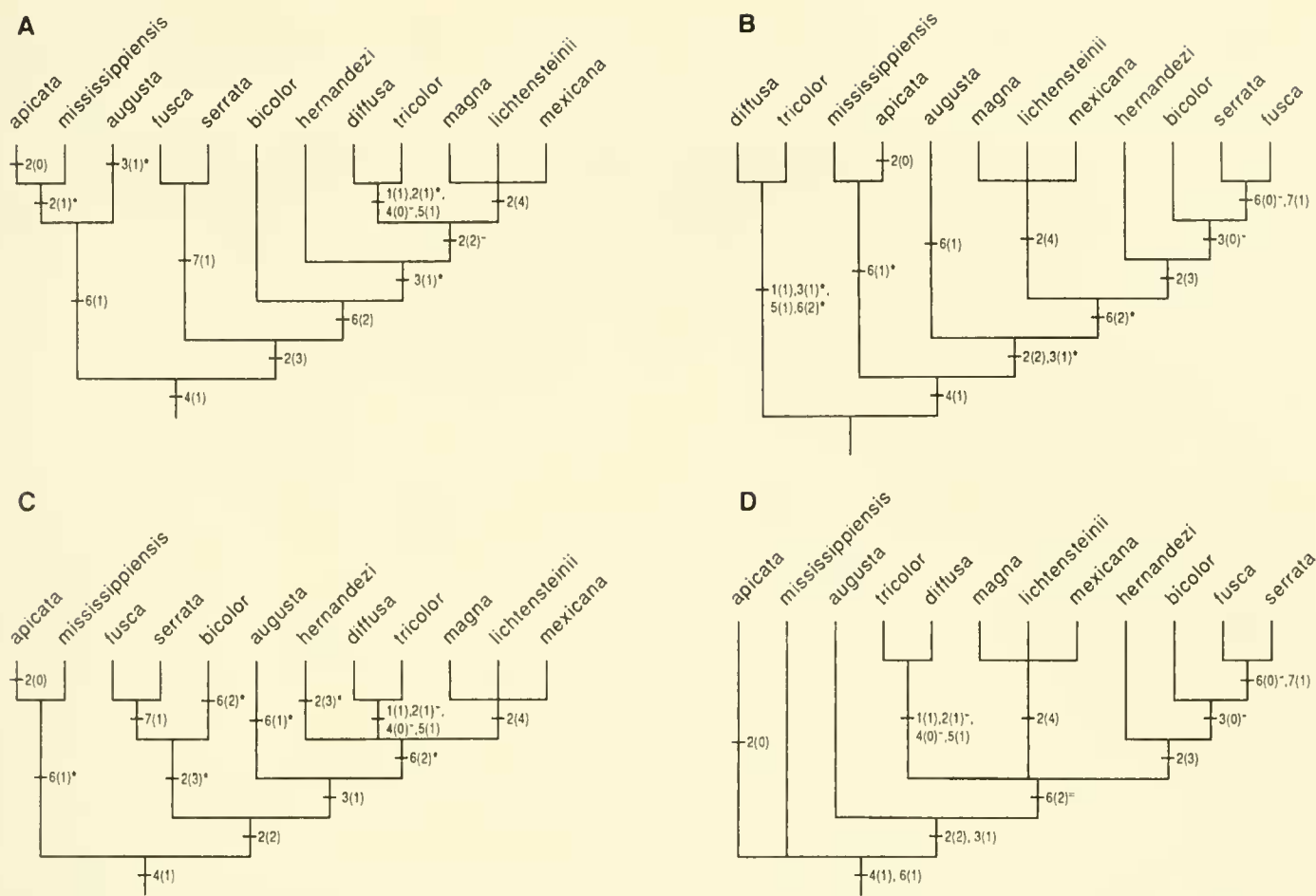


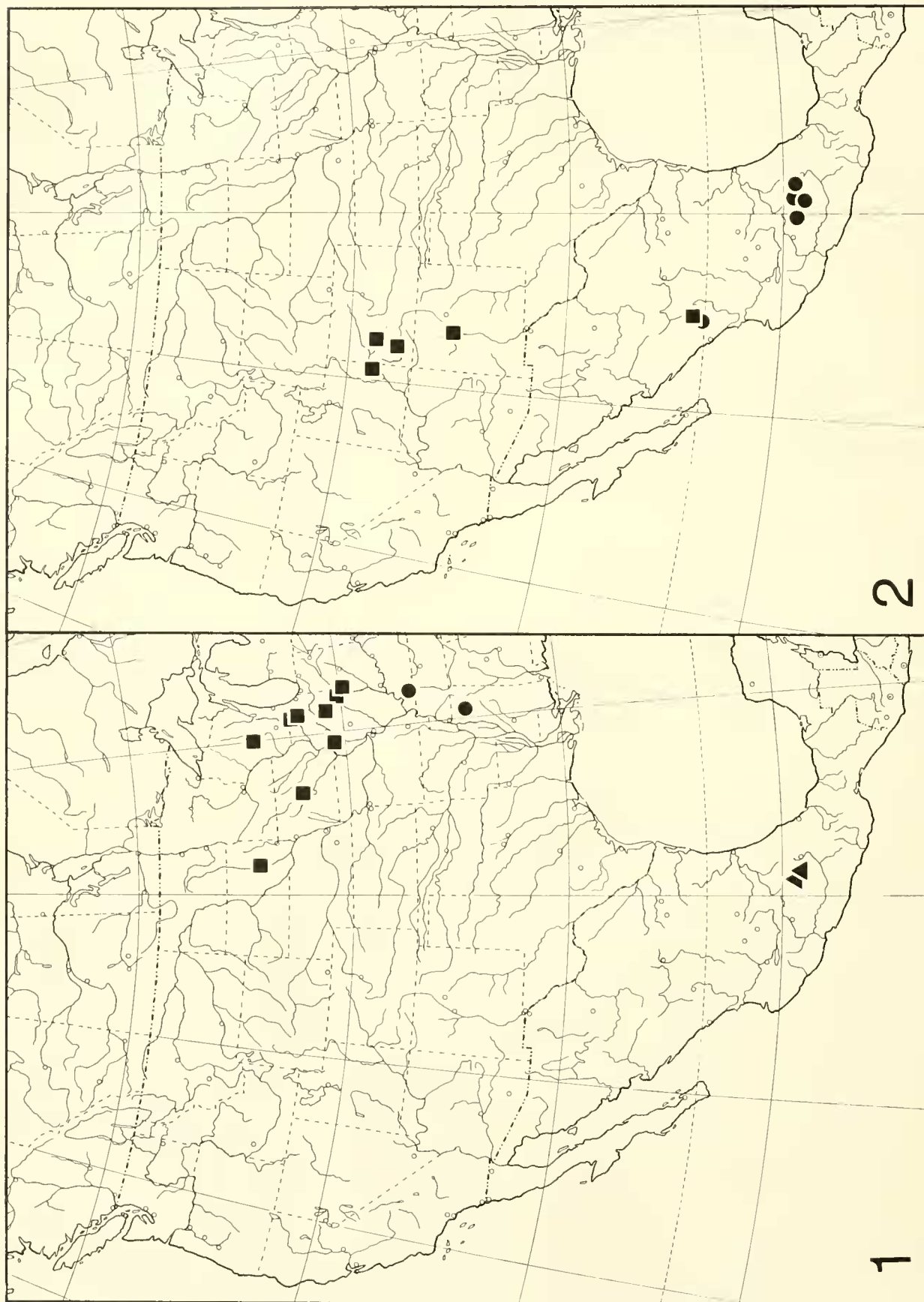
Fig. 4. Examples of hypotheses of phylogenetic relationships among the species of *Gymnocarena* if state 0 of character 5 is assigned to outgroup. A, single tree resulting if state 2 is assigned for character 2 (Table 2, outgroup C); B-D, 3 of 30 trees resulting if state 1 is assigned for character 2 (Table 2, outgroup D). Numbers and symbols are as in Fig. 1.

aceae, suggesting that *Gymnocarena* species may be restricted to this group. *Gymnocarena tricolor* (Doane) breeds in flower heads of *Helianthus tuberosus* and *H. grosseserratus* (W. B. Stoltzfus, pers. comm.), and *G. diffusa* has been reared from flower heads of *H. annuus* (wild and cultivated varieties), *H. maximiliani*, and *H. tuberosus*. Adults of *G. diffusa* also have been collected on *H. petiolaris*, but this plant is unconfirmed as a host. *Helianthus* species may be hosts of other *Gymnocarena* species; adults of *G. apicata* have also been collected on *H. annuus*. Other plants must be used by the *Gymnocarena* species occurring in central Mexico, however, as no *Helianthus* are known to occur there (except for *H. annuus* introduced for cultivation), and only a few extend into northern Mexico (Heiser et al. 1969). *Verbesina oncophora* is a host of *G. carinata*, and *Dahlia imperialis*, *D. merckii*, and possibly other *Dahlia* species are hosts

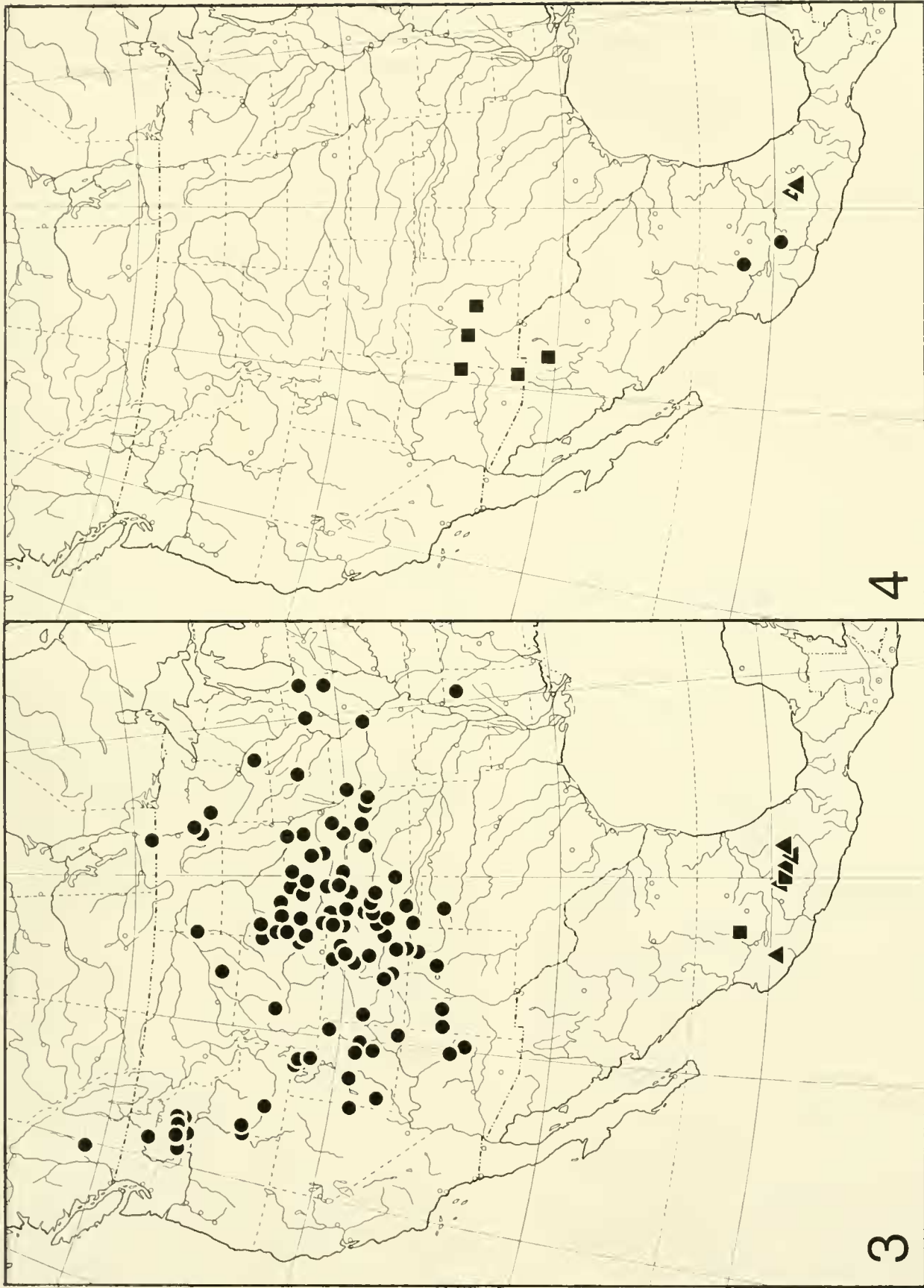
of *G. mexicana* (see "Biology" under those species).

According to Kamali and Schulz (1973, 1974) females of *G. diffusa* lay their eggs between involucre bracts of unopened sunflower capitula, and the larvae feed on the spongy tissue of the receptacle. They leave the flower to pupariate in the soil and overwinter in this stage. The larvae of *G. carinata* and *G. mexicana* also leave the capitulae of their hosts to pupariate. I made only casual observations of their feeding. The larvae of *G. carinata* consumed some developing seed tissues and most of the receptacle of *V. oncophora* capitulae. There is little receptacle tissue in *Dahlia* flowers, and the larvae of *G. mexicana* seem to consume mainly developing achenes and surrounding tissues in the basal half of the capitulum.

The pest status of *G. diffusa* is unclear, because the effect on seed production of the larval receptacle feeding, although obvious-



Maps 1-2. Localities of specimens examined. 1: *angusta* Norrbom (triangles), *mississippiensis* Norrbom (circles), and *tricolor* (Doane) (squares). 2: *apicata* (Thomas) (squares) and *mexicana* (Aczél) (circles).



Maps 3-4. Localities of specimens examined. 3: *diffusa* (Snow) (circles), *magna* Norrbom (squares), and *serrata* Norrbom (triangles). 4: *bicolor* Foote (squares), *carinata* Norrbom (hollow triangle), *fusca* Norrbom (solid triangle), and *hernandezii* Norrbom (circles).

ly deleterious, has not been well studied. Kamali and Schulz (1974) reported that infestation levels in sunflower cultivars averaged 56% in 1971–72 in North Dakota, but McBride et al. (1985) considered the damage to be negligible. In eastern Colorado, however, B.C. Kondratieff (pers. comm.) found that damage (less than 50% seed development) in cultivated sunflowers averaged between 26% and 49% in 1987–89.

DISTRIBUTION

The species of *Gymnocarena* occur from the central Nearctic Region to its southern extent in central Mexico (Maps 1–4). *Gymnocarena mississippiensis* is known only from the Mississippi Valley, and *G. tricolor* from the midwestern United States. *Gymnocarena diffusa* has the broadest range, from Illinois, southern Manitoba and British Columbia to Mississippi and Arizona. Its distribution and abundance probably have been increased by human cultivation of one of its hosts, *Helianthus annuus*. The remaining nine species of *Gymnocarena* are montane. *Gymnocarena apicata* occurs in the Rockies in Utah, Colorado, and New Mexico, with another population, possibly disjunct, in the Sierra Madre Occidental in Durango, whereas *G. bicolor* is known only from the mountains of Arizona, New Mexico, and Chihuahua. *Gymnocarena hernandezii*, *G. magna*, and *G. mexicana* are known from the Sierra Madre Occidental and the transverse volcanic belt of central Mexico, whereas *G. angusta*, *G. carinata*, *G. fusca*, and *G. serrata* have been collected only in the latter area. The type locality of *G. lichtensteinii* is not precisely known, but it is also probably from the volcanic belt. I have examined no *Gymnocarena* adults from the Sierra Madre Oriental or the Sierra Madre del Sur, although I have seen a puparium from *Dahlia* flowers in Oaxaca that may be *G. mexicana* or another *Gymnocarena* species (see *G. mexicana*, "Biology").

The distribution of *Gymnocarena* indicates that its evolution has been recent. Its absence from California suggests that it arose after the Middle Pliocene, and its distribution in Mexico fits the pattern of nearctic groups of recent (Pliocene-Pleistocene) penetration (Halffter 1987).

Genus *Gymnocarena* Hering

Gymnocarena Hering 1940: 4 (Type species: *Oedicarena diffusa* Snow, by original designation); Foote 1960: 112 [review], 1965: 675 [catalog], 1980: 30 [review, in key]; Wasbauer 1972: 117 [hosts]; Blanc and Foote 1987: 428 [review].

Tomoplagiodes Aczél 1954: 91 (Type species: *T. mexicana* Aczél, by original designation); Foote 1967: 48 [catalog], 1980: 30 [synonymy].

Mylogymnocarena Foote 1960: 111 (Type species: *Urellia apicata* Thomas, by original designation); Foote 1965: 669 [catalog]; Blanc and Foote 1987: 430 [review]. **NEW SYNONYMY.**

Description.—Body length 4.0–7.5 mm, not including female ovipositor. Cuticle yellow to orangebrown. Setae yellow to brown, never whitish or strongly expanded. Setulae yellow to brown, acuminate. **Head:** more or less quadrate in lateral view, frons and face usually meeting at angle of 90–105°, rarely as much as 120°; lunule wider than high; frons non-setulose medially; usually 3 pairs of frontal setae, 4–5 on one or both sides occasionally in *mexicana*, rarely in other species; 2 pairs of reclinate, unicolorous orbital setae; postocular setae slender to slightly swollen; genal height 0.23–0.50 times eye height; arista (Fig. 2) bare except for minute microtrichia on swollen basal part, usually with slight but distinct subapical bend. **Thorax:** entirely microtrichose, but not densely so; anepisternal cleft (internal sulcus) distinct; scapular setae undifferentiated or varied in number and location; typical setae present, including following

pairs: 1 postpronotal, 2 unicolorous notopleurals, 1 presutural and 1 postsutural supra-alar, 1 intra-alar, 1 postalar, 1 dorso-central, 1 acrostichal, 2 anepisternal, 1 katepisternal, 1 anepimeral; dorsocentral setae usually aligned with supra-alars or slightly anterior or posterior to them, sometimes distinctly posterior in *mexicana*, but always closer to supra-alars than to postalars or transverse suture; scutellum with 2 pairs of marginal setae, apical pair subequal to basal pair. *Legs*: hind femur with 1–3 anterodorsal and 1 posterodorsal preapical setae. *Wing*: light areas with faint pattern of gray and white microtrichia, or entirely with white microtrichia; vein R_1 entirely setulose dorsally, without gap near level of apex of sc; vein R_{4+5} setulose dorsally to beyond dm-cu, ventrally with at least 1–2 setulae basal to r-m, sometimes setulose to beyond r-m; cell bcu with distinct lobe, $\frac{1}{3}$ – $\frac{1}{2}$ as long as width of cell; r-m well beyond middle of cell dm. *Abdomen*: preabdominal terga and sterna entirely microtrichose. *Male genitalia*: epandrium and outer surstyli (Fig. 1C, E), in posterior view, nearly oval, in lateral view, margin of surstylus usually projected as dorsal lobe (Fig. 1B, D); hypandrial apodeme broad and flattened; lateral sclerite fused to hypandrium near level of arms of aedeagal apodeme, on left side less than $\frac{1}{5}$ as long as distance from anterior fusion point to base of hypandrium, on right side, $\frac{1}{2}$ to 1 times that distance; distiphallus (Fig. 1A) with numerous spinelike or scale-like projections on membranous apical part; endophallus short, stout, slightly curved. *Female terminalia*: 2 spermathecae (Fig. 7I); apical part of spermathecal duct (2–4 times length of spermatheca) dilated.

KEY TO SPECIES OF *GYMNOCARENA*

1. Cell r_{2+3} with basal $\frac{2}{3}$ light or with only very faint gray markings, without band between pterostigma and r-m (Fig. 5A–B) 2
- Cell r_{2+3} with basal $\frac{2}{3}$ largely yellow or brown, or at least with broad band between pterostigma and r-m (Fig. 5C–H) 3

2. Wing (Fig. 5A) with dark markings confined to apical third except for yellowish pterostigma; crossvein dm-cu narrowly bordered with dark brown; aculeus tip (Fig. 7B) slender, sharply acute (Durango to Utah and Colorado) *apicata* (Thomas)
- Wing (Fig. 5B) with dark brown mark extended from pterostigma into cell r_1 ; veins bm-cu, Cu_2 , and r-m narrowly bordered with brown, dm-cu broadly bordered with brown; aculeus tip (Fig. 8F) broader, blunt (Puebla to Durango) *mexicana* (Aczél)
3. Cell r_{4+5} with large basal or medial light area filling almost half or more of cell (Fig. 5C–D) 4
- Cell r_{4+5} more extensively dark, with or without several smaller medial light spots (Fig. 5E–H, 6A–F) 6
4. Cell r_{4+5} with large light area extended apical to midlength of cell, at most with tiny light spots apical to this (Fig. 5C–D); aculeus tip (at least in *magna*) blunt, broad, with sides concave 5
- Cell r_{4+5} with large light area not extended to midlength of cell, with round light spot half as wide as cell apical to its midlength; aculeus tip (Fig. 7A) acute, slender, with sides evenly tapered (Distrito Federal and Morelos) (see also couplet 7) *angusta*, n. sp.
5. Cell m with 4 white spots within faint gray area, usually arranged in rectangle, also with white spot within apical dark brown part of cell (Fig. 5C); aedeagus more than 3.0 mm long; female syntergosternite 7, measured dorsally, 1.87–2.41 mm long, 0.70–0.75 times as long as mesonotum (Mexico to Jalisco) *magna*, n. sp.
- Cell m with 3 white spots within faint gray area, arranged in triangle, apical dark brown part of cell without white spot (Fig. 5D); aedeagus less than 3.0 mm long; female unknown, but syntergosternite 7 probably shorter (Mexico) *lichtensteinii* (Wiedemann)
6. Cell r_1 , apical to pterostigma, with 2 light areas (Fig. 5F–H) or with 1 area with medial brown spot within it (Fig. 5E) 7
- Cell r_1 , apical to pterostigma, entirely dark or with 1 uninterrupted light area (Fig. 6) 10
7. Wing pattern (Fig. 5E) entirely brown; medial brown spot in cell r_1 small, not extended to vein R_{2+3} ; cell dm with basal half light; aculeus tip (Fig. 7A) slender, sharply acute (Distrito Federal and Morelos) (see also couplet 4) *angusta*, n. sp.
- Wing pattern (Fig. 5F–H) yellow and brown or entirely yellow; brown or yellow mark in cell r_1 extended to vein R_{2+3} ; cell dm with at

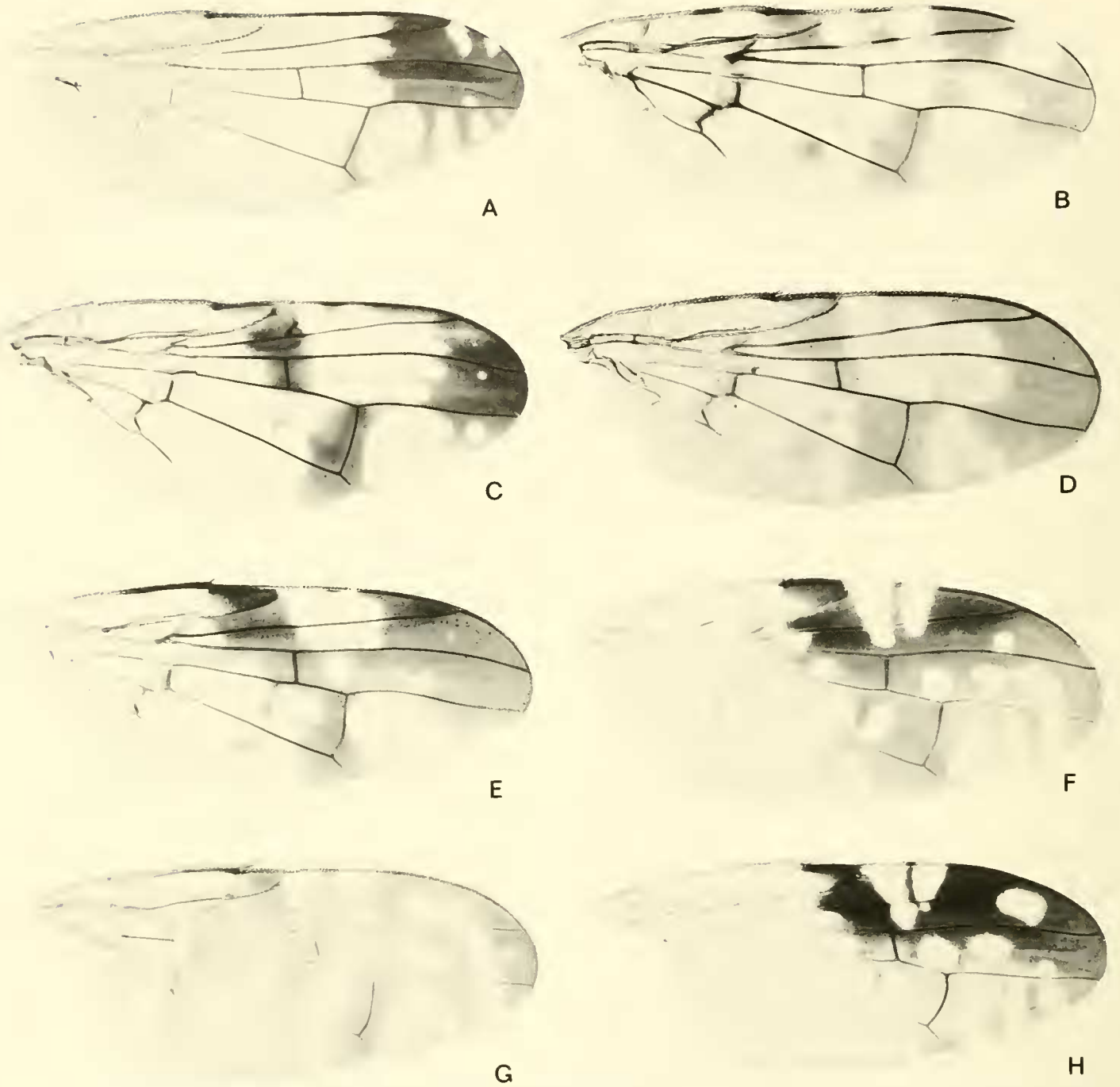


Fig. 5. Wings: A, *apicata* (Thomas), Durango: Tepalcates; B, *mexicana* (Aczél), Morelos: Lagunas de Zempoala; C, *magna* Norrbom, paratype, Jalisco: El Aguacate; D, *lichtensteini* (Wiedemann), lectotype; E, *angusta* Norrbom, paratype; F, *mississippiensis* Norrbom, holotype; G, *diffusa* (Snow), Iowa: Little Wall Lake; H, *tricolor* (Doane), Iowa: Ames (*flava* paratype).

- least basal one-sixth yellow; aculeus tip variable 8
- 8. Wing (Fig. 5G) with uninterrupted light band in cells r_{2+3} , br, and dm posterior to pterostigma, and with nearly complete light band between r-m and dm-cu, narrowly interrupted along vein M and sometimes along veins R_{2+3} and R_{4+5} ; aculeus tip (Fig. 8A) blunt, sides strongly concave, 8th sternites easily visible in dorsal view (eastern Washington to Manitoba and Illinois, south to New Mexico and Arizona *diffusa* (Snow)
- Wing (Fig. 5F, H) with isolated light spots in cells r_{2+3} , br, and dm posterior to pterostigma; light spots between r-m and dm-cu broadly separated at least along vein R_{4+5} and in cell dm; aculeus tip variable, but sides less concave and 8th sternites not or only slightly visible in dorsal view 9
- 9. Basal marginal light spot in cells r_1 and r_{2+3} with apex more or less even with r-m (Fig. 5F); r-m and dm-cu entirely bordered on both sides by dark brown; apical light spot in cell m extended well into cell r_{4+5} ; genal height

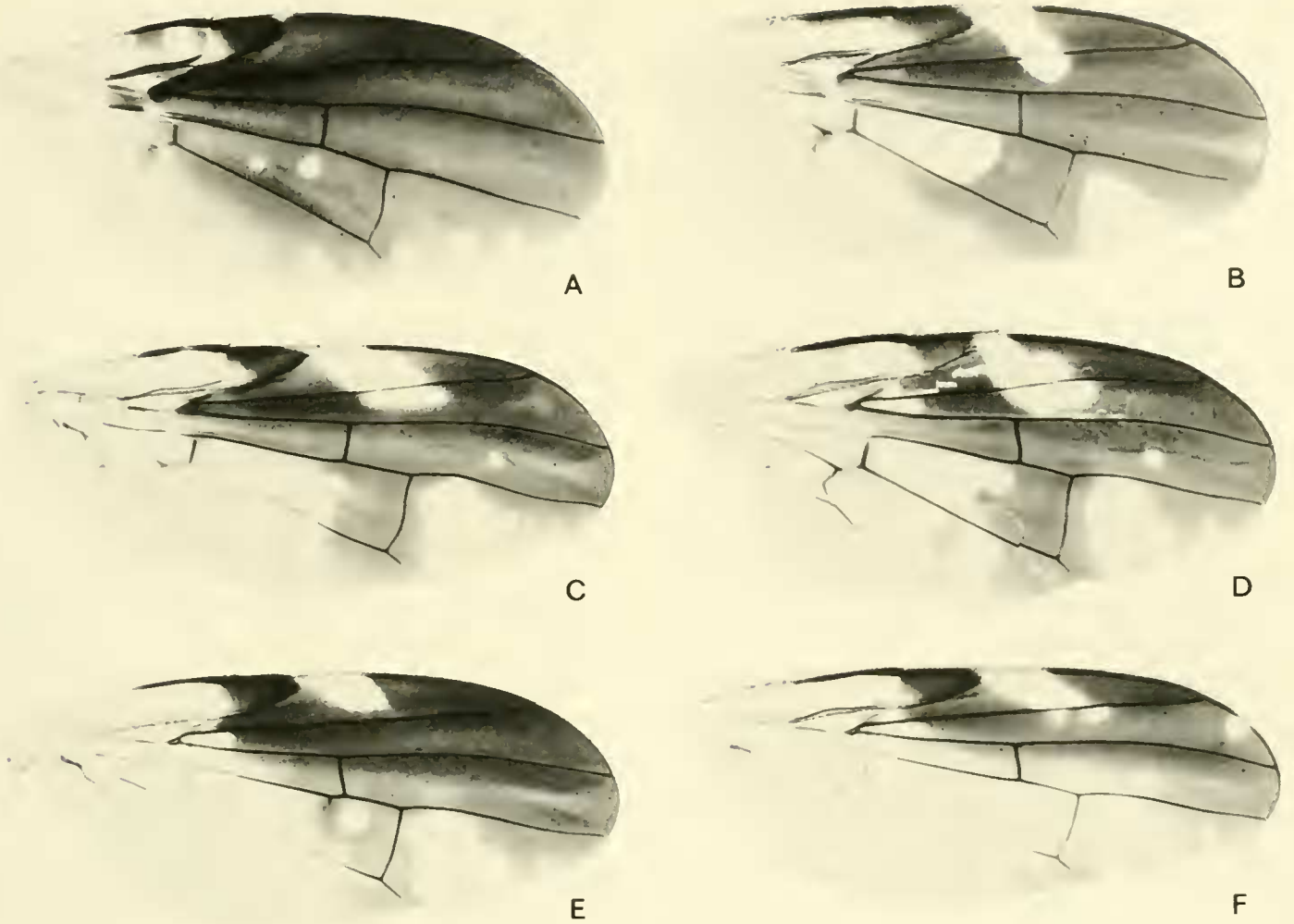


Fig. 6. Wings: A, *fusca* Norrbom, paratype; B, *bicolor* Foote, Chihuahua: Colonia Juarez; C, *hernandezii* Norrbom, paratype; D, sp. near *hernandezii*, Sinaloa: Potrerillos; E, *serrata* Norrbom, paratype, Morelos: Carretera Xochimilco-Oaxtepec; F same, paratype, Jalisco: Nevado de Colima.

- less than 0.35 times eye height; scutellum usually with tiny dark spots; aculeus tip (Fig. 7C) acute, sides evenly tapered (Mississippi and Kentucky) *mississippiensis*, n. sp.
- Basal marginal light spot in cells r_1 and r_{2+3} with apex apical to r-m (Fig. 5H); posterior half of r-m and all of dm-cu bordered on both sides by yellow; light spot in cell m not extended into cell r_{4+5} , although r_{4+5} sometimes with small spot opposite it; scutellum without tiny dark spots; genal height at least 0.35 times eye height; aculeus tip (Fig. 8B) blunt, sides concave (South Dakota to Wisconsin and Indiana) *tricolor* (Doane)
10. Cell r_1 with large marginal light spot (Fig. 6B-F); cells r_{2+3} and r_{4+5} often with small light spots; cell m with large basal marginal light spot extended to or almost to vein M; aculeus tip variable, but not sagittate 11
 - Cells r_1 , r_{2+3} , and r_{4+5} entirely dark brown (Fig. 6A); cell m with 3 small marginal light spots, none extended more than halfway to vein M; aculeus tip (Fig. 7F) sagittate, weakly serrate (Morelos) *fusca*, n. sp.
 11. Cell m with one large light spot with even margins, narrowly separated from vein M (Fig. 6B); vein Cu_1 bordered with brown in cell cu_1 along its entire length; cell r_{4+5} entirely brown; female sytergosternite 7 0.53 times as long as mesonotum; aculeus tip (Fig. 8C) blunt (Chihuahua, Arizona, New Mexico) *bicolor* Foote
 - Cell m with one to several light spots, one of which touches vein M (Fig. 6C-F); vein Cu_1 bordered by light area in cell cu_1 along most of its length; cell r_{4+5} usually with 1-2 small light spots; female sytergosternite 7 more than 0.70 times as long as mesonotum or aculeus tip acute 12
 12. Cell br entirely dark apical to bm-cu (Fig. 6C-D); cell r_{4+5} without basal light spot, but with medial light spot; base of cell r_{2+3} light or dark; aculeus tip, at least in *hernandezii* (Fig. 8D), nonserate, with extreme apex broad and blunt; female sytergosternite sometimes more than 2.00 mm long, 0.75 times length of mesonotum 13
 - Cell br at least partially light apical to bm-cu

- (Fig. 6E-F); cell r_{4+5} entirely dark, with only basal light spot, or with both basal and medial light spots; aculeus tip finely serrate, extreme apex slender; female syntergosternite 7 1.04–1.16 mm long, 0.40–0.57 times as long as mesonotum 14
13. Base of cell r_{2+3} entirely dark (Fig. 6C); aedeagus more than 3.0 mm long, more than 1.0 times as long as mesonotum; female syntergosternite 7 2.08 mm long, 0.75 times as long as mesonotum; aculeus tip (Fig. 8D) blunt (Michoacan and Jalisco) *hernandezi*, n. sp.
– Base of cell r_{2+3} light (Fig. 6D); aedeagus less than 3.0 mm long, less than 1.0 times as long as mesonotum; female unknown, but syntergosternite 7 probably shorter; (Sinaloa) sp. near *hernandezi*
14. Base of cell r_{2+3} with light spot (Fig. 6E-F); aculeus tip (Fig. 7D-E) dorsally without medial ridge; 8th sternites nonserrate apicolaterally (Puebla to Jalisco) *serrata*, n. sp.
– Base of cell r_{2+3} entirely dark; aculeus tip (Fig. 7G-H) dorsally with medial ridge; 8th sternites serrate apicolaterally (Distrito Federal) *carinata*, n. sp.

Gymnocarena angusta Norrbom,

NEW SPECIES

Figs. 5E, 7A, Map 1

Holotype: ♀ (USNM), MEXICO: MORELOS: Km. 49.5 Rt. 142 (Xochimilco-Oaxtepec), 5 km. N El Vigia, 30.IX.1991, A. L. Norrbom.

Paratype: ♀ (UNAM), MEXICO: DISTRICTO FEDERAL: Pedregal de San Angel, 20.VII.1968, C. Beutelspacher.

Diagnosis.—The wing pattern is intermediate between *G. magna* and *G. lichtensteinii*, which have a larger, more apically extended light area in the radial cells, and *G. hernandezi* and *G. serrata*, in which this light area is smaller and without a medial dark spot in cell r_1 . The slender, non-serrate aculeus tip readily distinguishes *G. angusta* from all of these species.

Description.—Setae yellowish to light brown, those on frons darkest. Setulae yellowish except on abdomen. *Head*: genal height 0.34–0.35 times eye height; facial carina moderately to well developed, ventral expanded part medium sized, its height $\frac{1}{3}$ that of face, in lateral view, margin of ventral part straight and more or less parallel

with margin of facial ridge or concave and projected anteriorly. *Thorax*: with small dark spots (faint in paratype), at least on scutellum; mesonotum 2.12–2.70 mm long; dorsocentral setae aligned with supra-alar setae. *Legs*: femora not unusually stout. *Wing* (Fig. 5E): with dark brown mark from pterostigma to r-m, another covering dm-cu, and a third broad apical dark area, these narrowly connected or narrowly separated in cell r_{4+5} ; largely light basal to these dark marks, with numerous white spots within gray areas (poorly differentiated in paratype); cell r_1 with broad light mark with irregular margin, extended into r_{2+3} or r_{4+5} , small brown spot within it along Costa; cell m with broad irregular light mark with 4–5 white spots and large faint medial brown spot within it; cell r_{4+5} with small light spot near its middle, largely light basally or mostly dark with large light spot anterior to dm-cu; cell r_{2+3} with small basal light area, apex entirely dark or with light spot at apex of R_{2+3} ; cell br with light spot posterior to pterostigma; cell dm mostly light, except apex and narrow medial brown spot. *Abdomen*: setulae on syntergum 1+2 yellowish except posteriorly; setulae on terga 3–5 brown. *Female terminalia*: syntergosternite 7 1.01–1.08 mm long, 0.40–0.48 times as long as mesonotum; aculeus 0.84–0.95 mm long, tip (Fig. 7A) slender, sides nonserrate, nearly straight, evenly tapered to slender, acute extreme apex; 8th sternites with apices normally not visible in dorsal view, lateral margins evenly rounded; spermathecae relatively large.

Remarks.—The wing pattern of the paratype is more extensively dark than that of the holotype, but considering their very similar aculei and the range of wing variation in other species (e.g. *G. serrata*), a hypothesis that they are conspecific seems reasonable.

Distribution.—(Map 1). Known only from the Distrito Federal and Morelos.

Etymology.—The epithet is a Latin adjective meaning narrow, in reference to the slender aculeus.

Gymnocarena apicata (Thomas),

NEW COMBINATION

Figs. 5A, 7B, Map 2

Urellia apicata Thomas 1914: 428 (Holotype ♀ (MCZ), USA: COLORADO; [with labels with "Colo. 2277," "Urellia apicata n. sp.," "Holotype no.," and "Type 7731"]).

Mylogymnocarena apicata: Foote 1960: 111 [taxonomy], 1965: 669 [catalog]; Wasbauer 1972: 118 [host catalog]; Dodson 1987: 614 [New Mexico]; Blanc and Foote 1987: 431 [review].

Diagnosis.—The highly reduced wing pattern, without dark markings basal to crossvein dm-cu, readily distinguishes this species. Only *G. angusta* and *G. mississippiensis* have a similarly slender aculeus.

Description.—Setae yellowish to light brown, those on frons typically darkest. Setulae yellowish except on abdomen and sometimes on scutellum. *Head*: genal height 0.37–0.41 times eye height; facial carina weakly to moderately developed, ventral part small or not expanded, in lateral view, margin of ventral part concave or projected anteriorly. *Thorax*: with or without small dark spots (present in 3 of 8 specimens, including type, but strong only in Durango male); mesonotum 2.41–2.62 mm long; dorsocentral setae aligned with supra-alar setae. *Legs*: femora not unusually stout. *Wing* (Fig. 5A): with dark brown apical spot, hyaline or faint gray basal to dm-cu, except pterostigma often yellowish or light brown; cell r_1 with apical $\frac{1}{4}$ – $\frac{1}{3}$ dark brown, often with tiny circular subapical white spot basal to dark area; cell r_{2+3} with oval white spot basal to dark area and with 2 marginal white spots; cell r_{4+5} with basal $\frac{1}{3}$ gray, with white spot basal to dark area, dark area with 1–2 tiny white spots within it; cell m with apex, 2 medial rays, and narrow ray over dm-cu and apex of vein Cu_1 dark brown, basal area mostly grayish with oval white spot bordering dark brown mark anteriorly, apical 2–3 light areas white. *Abdomen*: setulae on syntergum 1+2 yellowish except posteri-

orly; setulae on terga 3–5 brown. *Male terminalia*: outer surstylus without dorsal lobe; aedeagus 2.16 mm long, 0.82 times as long as mesonotum. *Female terminalia*: syntergosternite 7 1.08–1.16 mm long, 0.45–0.46 times as long as mesonotum; aculeus 0.92 mm long, tip (Fig. 7B) slender, sides non-serrate, nearly straight, evenly tapered to slender, acute extreme apex; 8th sternites normally not visible in dorsal view, lateral margins evenly rounded.

Remarks.—The holotype is the only specimen I examined with more than 3 pairs of frontal setae.

Biology.—This species has not been reared. Dodson (1987) collected adults on flowers of *Helianthus annuus*.

Distribution.—(Map 2). Utah and Colorado to Durango.

Specimens examined.—Holotype (see synonymy). MEXICO: DURANGO: Tepalcates, 30 mi W Durango, 8400 ft, 4–8.VIII.1972, J. Powell, D. Veirs & C.D. MacNeill, 1 ♂ (UCB). USA: COLORADO: San Juan Co.: S of Silverton, Molas-Elk Cr. Trails, 26–29.VII.1985, J. Jenkins, 1 ♀ (USNM); Gunnison Co.: Gothic, 9500 ft, 7.VIII.1972, C.L. Remington, 1 ♀ (MCZ). NEW MEXICO: Bernalillo Co.: VIII–IX.1981, G. Dodson, 2 ♀ (USNM). UTAH: Grand Co.: La Sal Mts., Warner Lake Campground, 10.VIII.1987, J. Jenkins, 1 ♀ (JJPC); San Juan Co.: La Sal Mts., nr. Warner Campground, 5–6.VIII.1985, J. Jenkins, 1 ♀ (USNM).

Gymnocarena bicolor Foote

Figs. 6B, 8C, Map 4

Gymnocarena bicolor Foote 1960: 113 (Holotype ♂ (USNM), USA: ARIZONA: Chiricahua Mountains, Indian Creek Canyon, 6100 ft); Foote 1965: 676 [catalog]; Wasbauer 1972: 117 [host catalog]. *Mylogymnocarena bicolor*: Blanc and Foote 1987: 431 [review].

Diagnosis.—*G. bicolor* is similar in wing pattern to *G. hernandezi* and *G. serrata*, which differ as indicated in the key. These

3 species are also distinguished by the shape of the aculeus tip, which in *G. bicolor* more closely resembles *G. tricolor* and *G. magna*.

Description.—Setae yellowish to brown, those on frons typically darkest. Setulae yellowish except on abdomen and sometimes on scutellum. *Head*: genal height 0.25–0.32 times eye height; facial carina weakly to moderately developed, ventral part small or not expanded, in lateral view, margin of ventral part concave or projected anteriorly. *Thorax*: usually with small dark spots, at least on scutellum (weak in N.M. ♂); mesonotum 1.87–2.25 mm long; dorsocentral setae slightly anterior to or aligned with supra-alar setae. *Legs*: femora not unusually stout. *Wing* (Fig. 6B): pattern mostly dark brown, faded in basal and anal cells and cell cu_1 ; largely infuscated apical to r-m; cell r_1 with 1 evenly margined, narrow white mark extended into cell r_{2+3} apical to r-m; cell m with large white mark with well defined margin, sometimes with small brown marginal spot within it; cell r_{2+3} without basal light area; cell br without light spot posterior to pterostigma; cell dm with large medial white spot, basal $\frac{1}{3}$ – $\frac{1}{5}$ faint gray or brown; cell cu_1 with small white spot near middle of vein Cu_2+A_1 , larger medial marginal white spot. *Abdomen*: setulae on syntergum 1+2 yellowish except posteriorly; setulae on terga 3–5 brown. *Male terminalia*: outer surstylus with small dorsal lobe; aedeagus 1.74–2.20 mm long, 0.93–0.98 times as long as mesonotum. *Female terminalia*: syntergosternite 7 1.08 mm long, 0.53 times as long as mesonotum; aculeus 0.79 mm long, tip (Fig. 8C) with sides nonserrate, moderately concave, slightly more constricted near apices of 8th sternites than in *tricolor*, extreme apex broad and blunt but tapered more rapidly than in *hernandezii*; 8th sternites with apices usually slightly exposed in dorsal view, lateral margins evenly rounded.

Distribution.—(Map 4). Chihuahua to Arizona and New Mexico.

Specimens examined.—Holotype (see

synonymy). MEXICO: CHIHUAHUA: Colonia Juarez, 5000 ft, 24.VIII.1979, G.S. Forbes, 1 ♂ (USNM). USA: ARIZONA: Apache Co.: St. Johns, 17.VIII.1935, I.J. Cantral, 1 ♀ (UMMZ). NEW MEXICO: Lincoln Co.: Lincoln, 24.VIII.1990, M.R. Pery, 1 ♂ (USNM). Socorro Co.: Magdalena Mts., 19.VIII.1951, E.L. Kessel, 1 ♂ (CAS).

Gymnocarena carinata Norrbom,

NEW SPECIES

Fig. 7G–H, Map 4

Holotype: ♀ (USNM), MEXICO: DISTRICTO FEDERAL: La Cima, reared ex. flowers of *Verbesina oncophora* (91M21) coll. 26.IX.1991, emerged I.1992, A. L. Norrbom.

Paratype: 1 ♂ (USNM), same data as holotype.

Diagnosis.—*G. carinata* is similar in wing pattern to *G. serrata*, *G. hernandezii*, and *G. bicolor*, which differ as indicated in the key. The aculeus tip differs from all *Gymnocarena* species in having a strong dorsal ridge, and from all species except *G. serrata* and *G. fusca* in having fine serrations. The serrations on the 8th sternites also distinguish it from all other species.

Description.—Setae yellowish brown. Setulae yellowish except on abdomen and scutellum and posteriorly on scutum. *Head*: genal height 0.26 times eye height; facial carina weakly developed, ventral part small, in lateral view, margin of ventral part concave and projected anteriorly. *Thorax*: with small dark spots on scutellum; mesonotum 2.12–2.18 mm long; dorsocentral setae aligned with supra-alar setae. *Legs*: femora not unusually stout. *Wing*: pattern dark brown anteriorly, posterior half mostly grayish or yellowish; cell r_1 with narrow white mark with distinct margin, without medial gray mark, and not extended into r_{2+3} ; cell r_{2+3} with small white spot near apex of r_1 spot and with small subapical white spot, entirely dark basally; cell m with 3 white spots, grayish anterobasally; cell r_{4+5} with posterior half of basal two-thirds gray-

ish, with small white spot anterior to dm-cu and another near middle; cell br mostly grayish, with or without small white spot posterior to pterostigma; cell dm with 3–4 white spots, greyish except apically. *Abdomen*: setulae on syntergum 1+2 yellowish except posteriorly; setulae on terga 3–5 brown. *Male terminalia*: not dissected. *Female terminalia*: syntergosternite 7 1.04 mm long, 0.48 times as long as mesonotum; aculeus 0.85 mm long, tip dorsally with medial ridge, best seen in lateral view (Fig. 7H), in ventral view (Fig. 7G), distinctly constricted just basal to apices of 8th sternites, beyond constriction gradually tapered, sides slightly concave, serrate almost to extreme apex; 8th sternites with apices well exposed in dorsal view, apicolateral margins serrate.

Remarks.—The type specimens are slightly teneral; their wings are not entirely unfolded and the pattern is perhaps not fully developed. The paratype is partially covered with fungus.

Biology.—I collected flowers of *Verbesina oncophora* B.L. Robins. and Greenm. at only one site. More than 30 larvae emerged and pupariated and were placed in moist vermiculite, but only the two type specimens emerged as adults. The puparia are stouter than those of *G. mexicana* and *G. diffusa*. Their surface is more wrinkled than in *G. diffusa*, but less than in *G. mexicana*.

Distribution.—(Map 4). Known only from the type locality in the Distrito Federal near the Morelos border.

Etymology.—The epithet is a Latin adjective meaning keeled, in reference to the dorsal ridge on the aculeus tip.

Gymnocarena diffusa (Snow)

Figs. 1A–C, 5G, 7I, 8A, Map 3

Oedicarena diffusa Snow 1894: 161 (Lectotype (designated by Foote 1962: 174) ♀ (UKaL), USA: KANSAS, Snow); Doane 1899: 179 [taxonomy]; Snow 1903: 219 [list]; Curran 1934: 290 [head]; Knowlton and Harmston 1937: 145 [Utah]; Byers et al. 1962: 180 [type data]; MacNay

1952a: 128 [Manitoba], 1952b: 197 [host], 1952c: 315, 1954: 361, 1956: 313; Bird and Mitchener 1954: 129 [Manitoba]; Bird and Robinson 1956: 46; Bird et al. 1959: 50; Beirne 1971: 60 [Manitoba].
Straussia diffusa: Coquillett 1899: 261 [taxonomy]; Essig 1926: 602 [distribution].
Strauzia diffusia: Cresson 1907: 100 [New Mexico]. [misspelling].
Spilographa diffusa: Aldrich 1905: 604 [catalog]; Washburn 1905: 118 [Minnesota].
Gymnocarena diffusa: Hering 1940: 4; Foote 1960: 113 [taxonomy, distribution], 1965: 676 [catalog]; Lipp and Schulz 1970: 27 [host, pest status]; Kamali and Schulz 1971: 85 [artificial diet], 1973: 288 [immature stages; North Dakota], 1974: 695 [biology]; Wasbauer 1972: 117 [hosts]; Hilgendorf and Goeden 1981: 105 [host]; Lisowski 1985: 105 [taxonomy; Illinois]; McBride et al. 1985: 9 [pest status]; Blanc and Foote 1987: 429 [review]; Charlet et al. 1989: 5 [host].

Diagnosis.—The wing pattern of *G. diffusa* is distinctive in that both the light and dark areas are long bands, rather than spots. Only *G. tricolor* also has stout femora and all abdominal setulae yellow.

Description.—Setae and setulae yellowish. *Head*: genal height 0.40–0.50 times eye height; facial carina moderately to well developed, ventral expanded part large, its height approximately ½ that of face, in lateral view, margin of ventral part straight to convex, more or less parallel with margin of facial ridge. *Thorax*: without small dark spots; scutal microtrichia slightly more dense than in other species, producing light gray appearance; mesonotum 2.66–3.49 mm long; dorsocentral setae more or less aligned with supra-alar setae. *Legs*: femora stout. *Wing* (Fig. 5G): pattern yellow to light brown, with numerous white bands, including uninterrupted one through cells r_{2+3} , br, and dm posterior to pterostigma, and subapical one across cells r_{4+5} and m, often fused with spot in cell r_{2+3} ; cell r_1 with 2 white

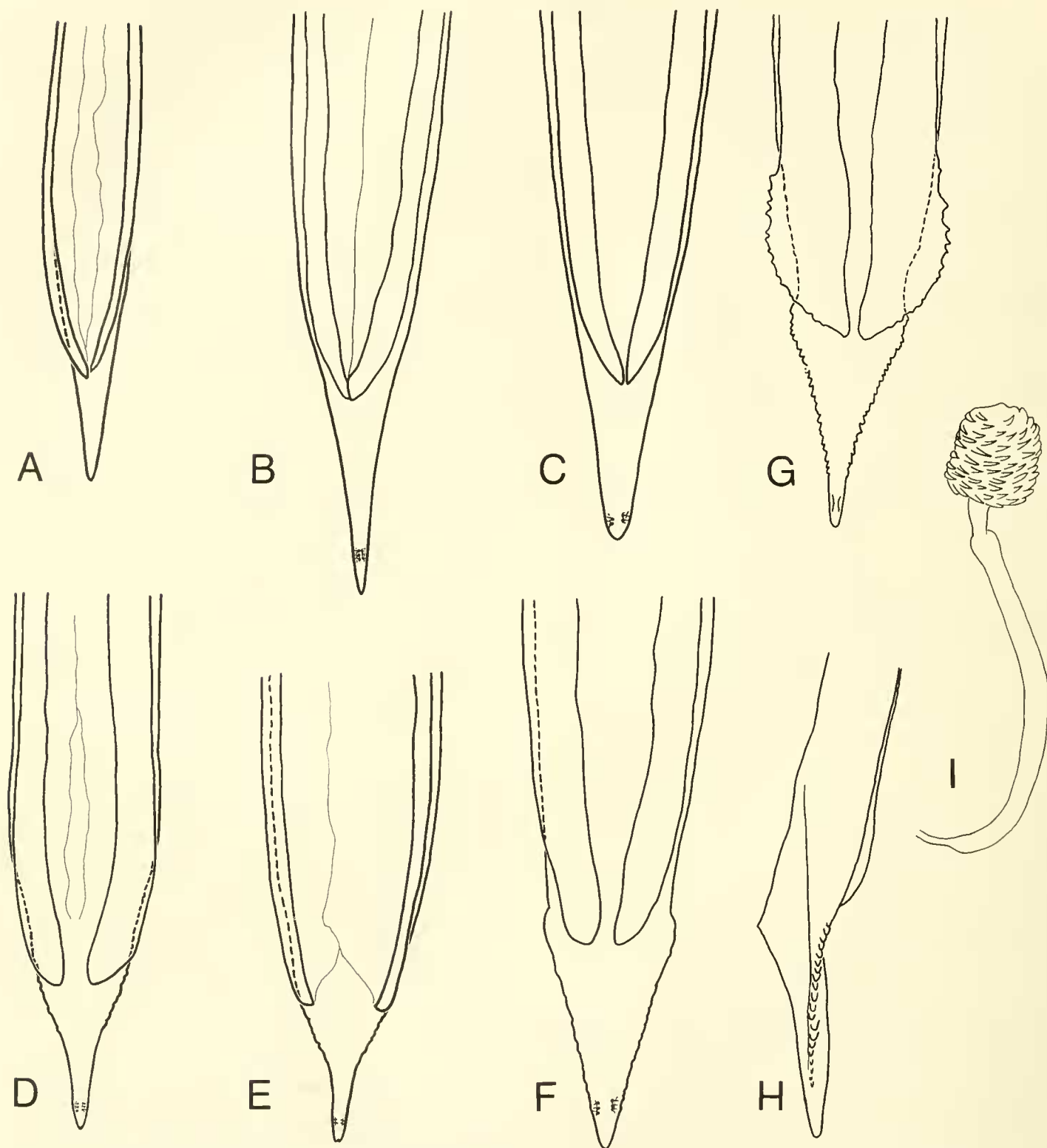


Fig. 7. Female terminalia: A, *angusta* Norrbom; B, *apicata* (Thomas); C, *mississippiensis* Norrbom; D-E, *serrata* Norrbom; F, *fusca* Norrbom; G-H, *carinata* Norrbom; I, *diffusa* (Snow); A-G, aculeus tip, ventral view; H, same, lateral view; I, spermatheca and apex of spermathecal duct.

marks, basal one extended into cell r_{2+3} basal to or even with $r-m$, apical one usually extended to vein M, occasionally narrowly interrupted along vein R_{2+3} or R_{4+5} ; cell r_{2+3} with extreme base yellow. *Abdomen*: setulae on all terga yellowish. *Male terminalia*: outer surstylus with large dorsal lobe (Fig. 1B-

C); aedeagus 3.62–3.95 mm long, 1.19–1.36 times as long as mesonotum. *Female terminalia*: syntergosternite 7 1.75–1.87 mm long, 0.52–0.61 times as long as mesonotum; aculeus 1.53–1.60 mm long, tip (Fig. 8A) with sides nonserrate, strongly concave, extreme apex broad and blunt; 8th sternites

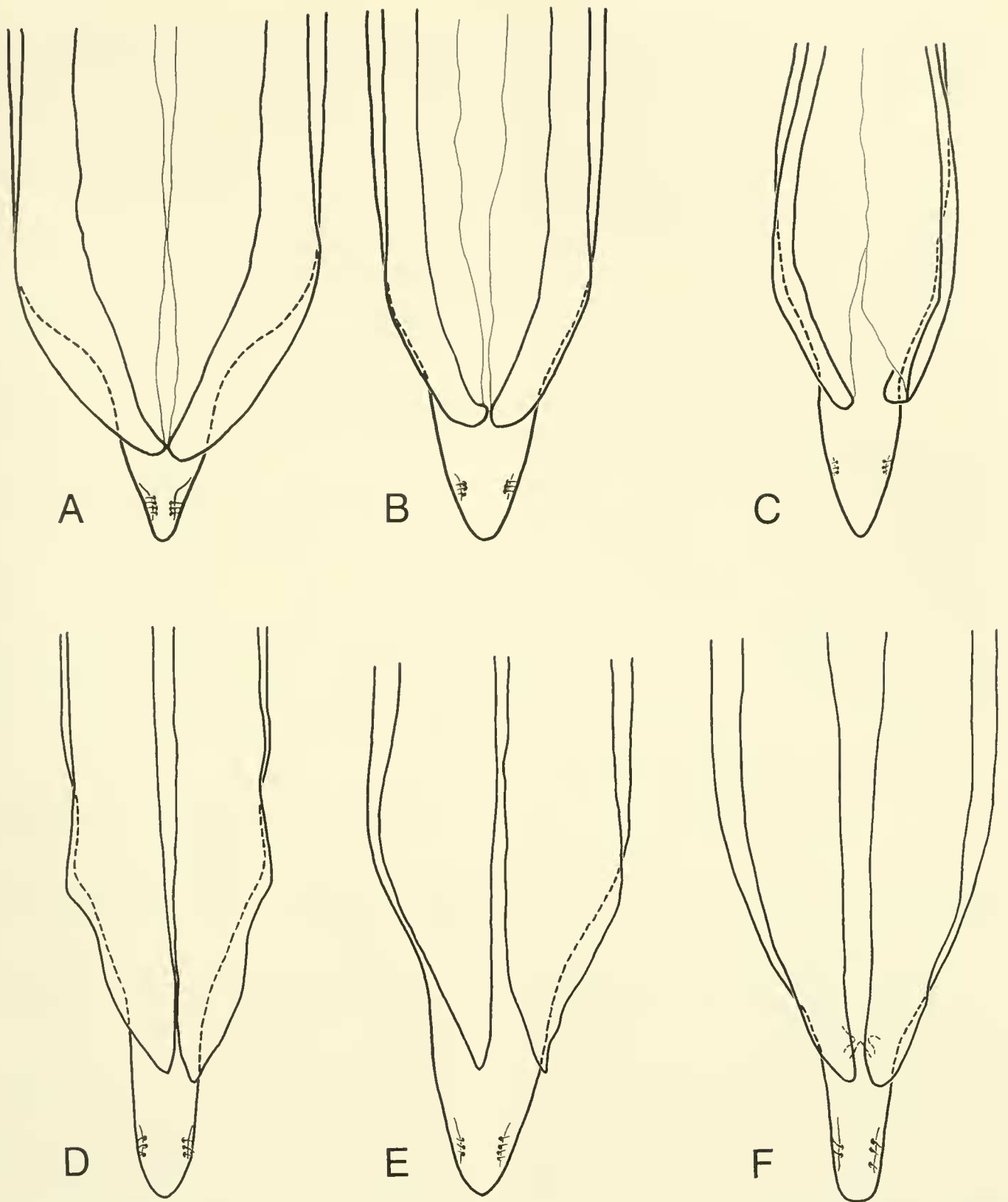


Fig. 8. Aculeus tip, ventral view: A, *diffusa* (Snow); B, *tricolor* (Doane); C, *bicolor* Foote; D, *hernandezi* Norrbom; E, *magna* Norrbom; F, *mexicana* (Aczél).

with apices broadly exposed in dorsal view, lateral margins evenly rounded.

Biology.—The known hosts are *Helianthus annuus* L., *H. maximiliani* Schrad. (MacNay 1952b, Kamali and Schulz 1973), and *H. tuberosus* L. (W. B. Stoltzfus, pers.

comm.), although examined specimens were also collected on *H. petiolaris* Nutt. Kamali and Schulz (1973, 1974) thoroughly described the immature stages, life cycle, and biology of this species (see “Host data” section).

Distribution.—(Map 3). British Columbia, Manitoba and Illinois, south to Mississippi and Arizona. Not reported from California or the Pacific coast. Dots on map 4 are based on examined specimens except for several localities reported by Kamali and Schulz (1974): Fargo, Hunter, and Casselton, Cass Co., N. Dakota, and Hendrum, Norman Co., Minnesota.

Specimens examined.—A complete list of specimens examined is available from the author. Specimens were seen from the localities indicated on Map 4 in the following states and provinces: CANADA: British Columbia, Manitoba; USA: Arizona, Colorado, Idaho, Illinois, Iowa, Kansas, Minnesota, Mississippi, Missouri, Montana, Nebraska, New Mexico, Nevada, Oklahoma, South Dakota, Texas, Utah, Washington, and Wyoming (ANSP, CAS, CDA, CNC, CSUFC, FLBPC, FMNH, FSCA, INSH, KSU, MSUEL, TAMU, UAE, UAT, UKaL, UNL, USNM, USU, WSU).

***Gymnocarena fusca* Norrbom,**

NEW SPECIES

Figs. 6A, 7F, Map 4

Holotype: ♀ (USU), MEXICO: MORELOS: 6 mi E Cuernavaca, 1.IX.1974, G. Bohart & W. Hanson.

Paratype: same as holotype, 1 ♀ (USNM).

Diagnosis.—The entirely dark radial cells, particularly cell r_1 , and the distinctively shaped aculeus tip distinguish *G. fusca* from all other *Gymnocarena* species.

Description.—Setae yellowish to brown, those on frons typically darkest. Setulae yellowish except on abdomen and scutellum. *Head*: genal height 0.23–0.25 times eye height; facial carina weakly to moderately developed, ventral part small or not expanded, in lateral view, margin of ventral part concave or projected anteriorly. *Thorax*: with small dark spots, at least on scutellum; mesonotum 2.58–2.70 mm long; dorsocentral setae slightly anterior to or aligned with supra-alar setae. *Legs*: femora

not unusually stout. *Wing* (Fig. 6A): almost entirely dark brown, faded in basal and anal cells; cell c with 2 whitish spots separated by medial brown band; radial cells entirely brown; cell m with 3 marginal white spots; cell cu_1 with 2 marginal white spots; cell dm with 1–2 small medial white spots. *Abdomen*: setulae on syntergum 1+2 yellowish except posteriorly; setulae on terga 3–5 brown. *Female terminalia*: syntergosternite 7 0.91–1.12 mm long, 0.35–0.41 times as long as mesonotum; aculeus 1.00 mm long, tip (Fig. 7F) sagittate, constricted just basal to apices of 8th sternites, beyond constriction sides weakly serrate, nearly straight and evenly tapered to acute extreme apex; 8th sternites with apices normally not visible in dorsal view, lateral margins evenly rounded.

Distribution.—(Map 4). Known only from the type locality in Morelos.

Etymology.—The epithet is a Latin adjective meaning dark, in reference to the mostly brown wing.

***Gymnocarena hernandezii* Norrbom,**

NEW SPECIES

Figs. 6C, 8D, Map 4

Mylogymnocarena sp.: Blanc and Foote 1987: 431.

Holotype: ♀ (UKaL), MEXICO: MICHOACAN: 5.3 mi SE Quiroga, 9.VIII.1963, G.W. Byers.

Paratype: MEXICO: JALISCO: El Aguacate, 14.7 mi SW Yahualica, 7700 ft, 12.IX.1986, D.K. Faulkner, 1 ♂ (SDNHM).

Diagnosis.—The wing pattern of *G. hernandezii* is similar to *G. bicolor*, *G. serrata*, and a probably undescribed species (see "Remarks"), which differ as indicated in the key. The shape of the aculeus tip is distinctive; it is broad, but not subapically constricted.

Description.—Setae yellowish to light brown, those on frons typically darkest. Setulae yellowish except on abdomen and

sometimes on scutellum. *Head*: genal height 0.25–0.27 times eye height; facial carina moderately to well developed, ventral part small or not expanded, in lateral view, margin of ventral part concave or projected anteriorly. *Thorax*: with small dark spots, at least on scutellum; mesonotum 2.78–2.87 mm long; dorsocentral setae slightly anterior to or aligned with supra-alar setae. *Legs*: femora not unusually stout. *Wing* (Fig. 6C): pattern mostly dark brown, faded in basal and anal cells and cell cu_1 to faint gray; largely infuscated apical to r-m; r_1 with broad whitish area extended into cell r_{2+3} apical to r-m, with faint brownish medial spot; cell r_{4+5} with small whitish spot near its middle; cell m with large faint gray medial area with 3–4 white spots at its corners, apical dark brown part of cell with 1 white spot; cell r_{2+3} without small basal light area; cell br without light spot posterior to pterostigma; cell dm with basal third faint gray, medially with 3–4 white spots; cells a_1 and cu_1 with several white spots within grayish area. *Abdomen*: setulae on syntergum 1+2 yellowish except posteriorly; setulae on terga 3–5 brown. *Male terminalia*: outer surstylus with small dorsal lobe; aedeagus 3.33 mm long, 1.16 times as long as mesonotum. *Female terminalia*: syntergosternite 7 2.08 mm long, 0.75 times as long as mesonotum; aculeus 1.33 mm long, tip (Fig. 8D) slightly constricted before broadest part, with sides nonserrate, moderately concave, extreme apex broad and blunt, very gradually tapered; 8th sternites with apices usually slightly exposed in dorsal view, sides with distinct corner slightly apical to level of constriction in aculeus.

Remarks.—A male from Sinaloa (Hwy. 40, 6.5 mi E Potrerillos, 21.VIII.1964, E.I. Schlinger) in the collection of the UCR keys here, but probably represents another undescribed species. It differs from *G. hermandezi* as follows: the aedeagus is shorter (2.29 mm long, 0.89 times as long as mesonotum); the base of cell r_{2+3} is light (Fig.

6D); the light spot in r_1 is more irregular; and there is a subbasal white spot in cell dm. I am reluctant to formally describe it from only the male sex.

Distribution.—(Map 4). Jalisco and Michoacan.

Etymology.—I am pleased to name this species for my colleague Vicente Hernández Ortiz.

Gymnocarena lichtensteinii (Wiedemann),

NEW COMBINATION

Fig. 5D

Trypeta Lichtensteinii Wiedemann 1830: 497 (Lectotype (here designated) ♂ (ZMHU), MEXICO [probably DISTRITO FEDERAL, MEXICO, MORELOS or PUEBLA] [with 2 green labels with “Lichtensteinii Wied. *” and “Mexico. Deppe.” in handwriting that is not Wiedemann’s but matching that on most other types of his species in ZMHU, an orange “Type” label, and a white label with “2457”]); Loew 1862: 92 [taxonomy], 1873: 289 [taxonomy].

Trypeta (Icteric) Lichtensteinii: Loew 1873: 330.

Icteric Lichtensteinii: Loew 1873: 290.

Icteric lichtensteinii: Hendel 1914: 61 [catalog]; Aczél 1950: 273 [catalog].

Ictericodes lichtensteinii: Aczél 1952: 120 [catalog]; Foote 1967: 29 [catalog].

Diagnosis.—This species and *G. magna* are very similar in wing pattern; possibly only terminalia length will reliably distinguish them. See “Remarks”; also see “Diagnosis” for *G. magna*.

Description.—Setae yellowish. Setulae yellowish except on abdomen and a few on scutellum. *Head*: genal height 0.28 times eye height; facial carina moderately developed, ventral expanded part medium sized, its height almost $\frac{1}{4}$ that of face, in lateral view, margin of ventral part straight, slightly projected. *Thorax*: with small dark spots on scutellum; mesonotum 2.38 mm long;

dorsocentral setae slightly anterior to supra-alar setae. *Legs*: femora not unusually stout. *Wing* (Fig. 5D): pattern largely faint gray with white spots; broad dark brown bands from pterostigma to r-m and from vein M to posterior margin along dm-cu, these narrowly connected along vein M; broad dark brown apical spot, without apical light spot in cell r_{2+3} ; cell r_1 with narrow brown spot, fused with broad extension from apical brown spot along Costa, dividing large light area extended from cells r_{2+3} and r_{4+5} ; the latter light area largely faint gray with 7 peripheral white spots; cell m with 3 white spots within faint gray area, arranged in triangle, apical dark brown part of cell without light markings; cells r_{2+3} , br, and dm light basal to band over r-m, br with 1 subapical, dm with 2 medial, and cu_1 with 2 white spots. *Abdomen*: setulae on syntergum 1+2 yellowish except posteriorly; setulae on terga 3–5 brown. *Male terminalia*: outer surstylus with small dorsal lobe; aedeagus 2.70 mm long, 1.13 times as long as mesonotum.

Remarks.—Wiedemann (1830) did not state the number of males he examined, so I regard the single specimen now in the ZMHU as a syntype, and designate it as a lectotype. This specimen is possibly conspecific with those I have recognized as *G. magna*, but the differences in wing pattern and especially aedeagus length suggest that they are distinct. As the female terminalia in *Gymnocarena* are more diagnostic than those of the male, corroboration of this hypothesis may depend upon the collection of females matching the lectotype in wing pattern. These presumably will have a shorter syntergosternite 7 than *G. magna* if there are two distinct species.

Distribution.—The type locality was not specified within Mexico, but it is probably within the Distrito Federal, or the states of Mexico, Puebla, or Morelos. According to Papavero (1971), Deppe collected during 1824–27 and 1829 in these states as well as Veracruz. He also made one trip to Oaxaca, but as no other *Gymnocarena* are known

from the latter two states, it is unlikely that the lectotype of *lichtensteinii* came from them.

Gymnocarena magna Norrbom,

NEW SPECIES

Figs. 5C, 8E, Map 3

Holotype: ♀ (SDNHM), MEXICO: JALISCO: El Aguacate, 14.7 mi SW Yahualica, 7700 ft, 14.IX.1986, D. K. Faulkner.

Paratypes: same as holotype, 2 ♀ (SDNHM) 1 ♂ 2 ♀ (USNM). MEXICO: MEXICO: El Yukon, 20 km W Toluca, 8800 ft, 8.VIII.1962, G. L. Bush, 1 ♂ (USNM) 1 ♀ (MSUEL).

Diagnosis.—This species and *G. lichtensteinii* are very similar in wing pattern and are recognized mainly by differences in terminalia length (see "Remarks" for *G. lichtensteinii*). Both differ from *G. mexicana* in having the dark pterostigmal band extended to r-m, and from *G. angusta* by the larger, more apically extended light area in the radial cells. In addition, *G. magna* differs from both of these species in the shape of its aculeus tip, which more closely resembles *G. tricolor* and *G. bicolor*.

Description.—Setae yellowish to light brown, those on frons typically darkest. Setulae yellowish except on abdomen and sometimes on scutellum. *Head*: genal height 0.31–0.39 times eye height; facial carina moderately to well developed, ventral expanded part medium sized, its height $\frac{1}{4}$ – $\frac{1}{2}$ that of face, in lateral view, margin of ventral part straight, more or less parallel with margin of facial ridge or slightly projected. *Thorax*: usually with small dark spots, at least on scutellum; mesonotum 2.33–3.53 mm long; dorsocentral setae slightly anterior to slightly posterior to supra-alar setae. *Legs*: femora not unusually stout. *Wing* (Fig. 5C): pattern largely faint gray with white spots; broad dark brown bands from pterostigma to r-m and from vein M to posterior margin along dm-cu, these narrowly connected along vein M; broad dark brown apical spot, with at most 1 tiny apical light spot

in cell r_{2+3} ; cell r_1 with narrow brown spot, usually separate from narrow extension from dark apical spot along Costa, at least partially dividing light area extended from cells r_{2+3} and r_{4+5} ; the latter light area largely grayish with 8–12 white spots; cell m with 4 or more white spots within faint gray area, usually arranged in rectangle, apical dark brown part of cell with 1–2 white spots; cells r_{2+3} , br , and dm light basal to band over $r-m$, br often with subapical, dm with 3–4 medial, and cu_1 with 3–6 white spots. *Abdomen*: setulae on syntergum 1+2 yellowish except posteriorly; setulae on terga 3–5 brown. *Male terminalia*: outer surstylus with medium sized dorsal lobe; aedeagus 3.41–3.95 mm long, 1.12–1.46 times as long as mesonotum. *Female terminalia*: syntergosternite 7 1.87–2.41 mm long, 0.71–0.75 times as long as mesonotum; aculeus 1.62 mm long, tip (Fig. 8E) similar to *tricolor*, with sides nonserrate, moderately concave, extreme apex broad and blunt; 8th sternites with apices at most slightly exposed in dorsal view, lateral margins evenly rounded.

Distribution.—(Map 3). Jalisco and the state of Mexico.

Etymology.—The epithet is a Latin adjective meaning large, in reference to the size of this species.

Gymnocarena mexicana (Aczél)

Figs. 1D–E, 2, 5B, 8F, Map 2

Tomoplagiodes mexicana Aczél 1954: 91 (Holotype ♂ (USNM), MEXICO: DISTRITO FEDERAL, VII–VIII.1910).

Tomoplagiodes mexicanus: Foote 1967: 48 [catalog].

Gymnocarena mexicana: Foote 1980: 30 [taxonomy].

Diagnosis.—The small size of the dark pterostigmal band is diagnostic for *G. mexicana*. This mark is absent (*G. apicata*) or extended to $r-m$ in other species of *Gymnocarena* with reduced wing patterns. The dorsal teethlike structures on the aculeus are unique to this species.

Description.—Setae light to dark brown. Setulae generally brown except on postgena, parts of thoracic pleura and legs. *Head*: genal height 0.42–0.48 times eye height; facial carina moderately to well developed, ventral expanded part medium sized, its height $\frac{1}{5}$ – $\frac{1}{2}$ that of face, in lateral view, margin of ventral part straight, more or less parallel with margin of facial ridge or slightly projected. *Thorax*: usually with small dark spots, at least on scutellum; mesonotum 2.20–3.45 mm long; dorsocentral setae aligned with to distinctly posterior to supraalar setae, but never more than $\frac{1}{2}$ distance from them to postalar setae. *Legs*: femora not unusually stout. *Wing* (Fig. 5B): pattern largely hyaline or faint gray with white spots, except for following dark brown areas: pterostigma and cell r_1 posterior to it, narrow bands along $bm-cu$, Cu_2 , and $r-m$, broad band along $dm-cu$, medial spot in r_1 , spot on Cu_1 , medial spot in r_{4+5} , and broad apical band extended from r_1 to m , interrupted by large apical white spot in r_{2+3} touching apex of R_{2+3} ; r_{2+3} rarely with second marginal white spot; cell m with 2–3 white spots within medial grayish area. *Abdomen*: setulae on syntergum 1+2 yellowish except posteriorly; setulae on terga 3–5 brown. *Male terminalia*: outer surstylus with small dorsal lobe (Fig. 1D–E); aedeagus 2.91–3.33 mm long, 0.94–1.13 times as long as mesonotum. *Female terminalia*: syntergosternite 7 0.95–1.21 mm long, 0.32–0.44 times as long as mesonotum; aculeus 1.01–1.19 mm long, tip (Fig. 8F) with 3 teethlike projections on dorsal side near apices of 8th sternites, sides nonserrate, moderately concave, extreme apex broad and blunt, very gradually tapered; 8th sternites with apices at most slightly exposed in dorsal view, lateral margins evenly rounded.

Biology.—I collected more than 50 adults at Lagunas de Zempoala in mid August, 1989, only on or near plants of *Dahlia imperialis* Roetzl ex. Ort., or to a lesser extent on *D. merckii* Lehm. Only a few plants were beginning to flower at that time, and no flies

were reared from the samples collected. In late September and early October, 1991, numerous larvae were collected from flowers of both of the above species at this site. Other larvae were collected from flowers of *D. imperialis* near Angangueo, Michoacan and from flowers of *D. merckii* at Km. 42–43, Rt. 95 (libre), Distrito Federal. These are presumably *G. mexicana*. Like larvae of *G. diffusa*, they left the capitulae to pupariate. The puparia differ from those of *G. diffusa* in having more distinct segmentation and a more wrinkled, less punctate surface. They are very distinct from puparia of *Laksyetsa trinotata* Foote, which also attack *D. imperialis* at the Lagunas de Zempoala site; *L. trinotata* puparia are much broader posteriorly, being slightly egg or pear shaped, and they also usually remain inside the capitulum. I examined two puparia that may be *G. mexicana* from two other *Dahlia* species. No adults emerged from them, but they closely resemble the puparia of *G. mexicana* from Lagunas de Zempoala. One is from samples of *Dahlia coccinea* Cav. I collected from along Route 190 in the state of Mexico in August, 1989. The other was in the USNM collection with the type series of *Laksyetsa trinotata* and has the same label data, from Llano de las Flores, Oaxaca, from flower head of *Dahlia tenuicaulis*. As noted above, the puparia of *L. trinotata* from Lagunas de Zempoala are much different in appearance, and I doubt that the Oaxaca specimen is that species. These latter two *Dahlia* species may also be host plants of *G. mexicana* or at least of some *Gymnocarena* species. It is fitting that a species with the name *mexicana* breeds in *Dahlia*, the national flower of Mexico.

Distribution.—(Map 2). Durango to Morelos and Puebla. Possibly also in Oaxaca (see "Biology").

Specimens examined.—Holotype (see synonymy). MEXICO: DISTRITO FEDERAL: Pedregal de San Angel, 12.VII.1979, J. Butze, 1 ♂ (UNAM); La Cima, 18.VII.1984, G. Arzate, 1 ♂ (UNAM). DU-

RANGO: 17 mi NE El Salto, 21.VII.1982, 1 ♂ (SDNHM). MICHOACAN: 3.5 km N of Angangueo, 4.X.1991, A.L.Norrbom, 1 ♀ (USNM). MORELOS: Parque Nacional Lagunas de Zempoala, 9200 ft, 11.VIII.1962, G.L. Bush, 1 ♂ 1 ♀ (MSUEL) 1 ♀ (USNM); same, 9400 ft, 22.VIII.1969, G. W. Byers, 1 ♀ (UKaL); same, clearing and ravine at entrance and path along Lago de Zempoala, on *Dahlia imperialis* or *D. merckii*, 9–11.VIII.1989, A.L. Norrbom, 37 ♂ 9 ♀ (USNM) 10 ♂ 2 ♀ (UNAM, IEXV). PUEBLA: 15 mi NW San Martin, 9000 ft, 26.VII.1963, G.W. Byers, 1 ♂ (UkaL).

Gymnocarena mississippiensis

Norrbom, NEW SPECIES

Figs. 5F, 7C, Map 1

Gymnocarena tricolor: Blanc and Foote 1987: 429 [misidentification].

Holotype: ♀ (AMNH), USA: MISSISSIPPI: Lafayette Co.: Oxford, VI.1943.

Paratypes: KENTUCKY: Lyon Co.: Golden Pond, 25.V–25.VI.1964, M. Tidwell, 1 ♀ (FSCA). MISSISSIPPI: Lafayette Co., V–VI.1960, F.M. Hull, 1 ♂ (CNC); Oxford, VI.1943, 1 ♀ (USNM).

Diagnosis.—*G. mississippiensis* differs from other *Gymnocarena* species except *G. tricolor* in having a bicolored yellow and brown wing pattern with 2 distinct light triangles in cells r_1 and r_{2+3} (see key to distinguish these two species). It resembles *G. apicata* and *G. angusta* in aculeus shape.

Description.—Setae yellowish. Setulae yellowish except on abdomen. *Head*: genal height 0.25–0.34 times eye height; facial carina weakly to moderately developed, ventral part small or not expanded, in lateral view, margin of ventral part concave or projected anteriorly. *Thorax*: usually with small dark spots, at least on scutellum (3 of 4 specimens); mesonotum 2.16–2.41 mm long; dorsocentral setae slightly anterior to aligned with supra-alar setae. *Legs*: femora not unusually stout. *Wing* (Fig. 5F): pattern bicolored, mostly dark brown, but yellow

in basal cells and parts of cells br, dm, and cu₁; r-m and dm-cu bordered only by dark brown; cell r₁ with 2 white marks, basal always and apical usually extended into r₂₊₃, apex of basal mark even with r-m; cell r₂₊₃ with white spot along R₄₊₅ opposite apex of R₁, sometimes (2 Mississippi paratypes) extended broadly to margin at apex of R₁; cell m with 3 white marks, at least apical one broadly extended into cell r₄₊₅; cell r₄₊₅ with large white spot anterior to dm-cu; cell r₂₊₃ with small basal white area; cell br with white spot posterior to pterostigma; cell dm with 2 medial white spots.

Abdomen: setulae on syntergum 1+2 yellowish except sometimes posteriorly; setulae on terga 3–5 light brown. *Male terminalia*: outer surstylus with small dorsal lobe; aedeagus 2.50 mm long, 1.16 times as long as mesonotum. *Female terminalia*: syntergosternite 7 1.46 mm long, 0.61 times as long as mesonotum; aculeus 1.28 mm long, tip (Fig. 7C) slender, sides nonserrate, nearly straight, evenly tapered to acute extreme apex, slightly broader and blunter than in *angusta* and *apicata*; 8th sternites normally not visible in dorsal view, lateral margins evenly rounded.

Remarks.—The USNM paratype is missing its head. Also see “Remarks” for *G. tricolor*.

Distribution.—(Map 1). Mississippi and Kentucky.

Etymology.—The epithet is derived from the state of the type locality.

Gymnocarena serrata Norrbom,

NEW SPECIES

Figs. 6E–F, 7D–E, Map 3

Holotype: ♀ (UNAM), MEXICO: MORELOS: Km 49.5 Carretera Xochimilco-Oaxtepec [Rt. 142, 5 km. N El Vigia], 6.X.1984, A. Ibarra.

Paratypes: same as holotype, 9 ♀ (UNAM) 6 ♀ (USNM); same locality, 30.IX.1991, A. L. Norrbom, 1 ♂ 1 ♀ (USNM). MEXICO: DISTRITO FEDERAL: Ajusco, 1.X.1984, A. Ibarra, 1 ♀ (USNM). MICHOACAN:

3.5 km N of Angangueo, 4.X.1991, A.L.Norrbom, 1 ♂ (USNM). JALISCO: Parque Nacional Nevado de Colima, 10.7 mi N Hwy. 54, 8200 ft, 18.IX.1986, 1 ♀ (SDNHM). PUEBLA: 15 mi NW San Martin, 9000 ft, 26.VII.1963, G.W. Byers, 1 ♀ (UKaL).

Diagnosis.—*G. serrata* is similar in wing pattern to *G. hernandezi* and *G. bicolor*, which differ as indicated in the key. The shape of the aculeus tip, which is very finely serrate subbasally, is unique.

Description.—Setae yellowish to brown, those on frons typically darkest. Setulae yellowish except on abdomen and scutellum. *Head*: genal height 0.25–0.35 times eye height; facial carina weakly to moderately developed, ventral part small or not expanded, in lateral view, margin of ventral part concave or projected anteriorly. *Thorax*: usually with small dark spots, at least on scutellum (17 of 19 specimens); mesonotum 1.83–2.58 mm long; dorsocentral setae slightly anterior to aligned with supraalar setae. *Legs*: femora not unusually stout. *Wing* (Fig. 6E–F): pattern mostly dark brown, faded in basal and posterior parts of wing; largely infuscated apical to r-m; cell r₁ with single broad white mark with distinct margin, without medial faint gray mark, often not extended into r₂₊₃; cell r₂₊₃ sometimes with small medial apical white spot; cell m with 2–4 irregular white spots; cell r₄₊₅ usually with small white spot anterior to dm-cu, sometimes also with small white spot near middle (no specimens had only the latter spot), sometimes entirely dark; cell r₂₊₃ with small basal white area; cell br with white spot posterior to pterostigma, pattern faint in basal half; cell dm with 2–3 white spots in apical half, pattern faint in basal half. *Abdomen*: setulae on syntergum 1+2 yellowish except posteriorly; setulae on terga 3–5 brown. *Male terminalia*: outer surstylus with small dorsal lobe; aedeagus 1.72–2.27 mm long, 0.88–0.94 times as long as mesonotum. *Female terminalia*: syntergosternite 7 1.04–1.16 mm long, 0.45–

0.57 times as long as mesonotum; aculeus 0.83–0.96 mm long, tip (Fig. 7D–E) slightly constricted just basal to apices of 8th sternites, beyond constriction sides concave and weakly serrate to about midpoint, extreme apex slender, acute or with minute concavity; 8th sternites with apices usually slightly exposed in dorsal view, lateral margins evenly rounded.

Remarks.—The specimens from Morelos and the Distrito Federal have slightly more extensively dark wings than those from Jalisco, Michoacan, and Puebla, lacking the apical light spot in cell r_{2+3} and sometimes 1 or both spots in cell r_{4+5} . They are all assumed to be conspecific without further morphological or biological evidence to the contrary.

Distribution.—(Map 3). Jalisco to Morelos and Puebla.

Etymology.—The epithet is a Latin adjective meaning sawtoothed, in reference to the serrate aculeus.

Gymnocarena tricolor (Doane)

Figs. 5H, 8B, Map 1

Euaresta tricolor Doane 1899: 191 (Lectotype (designated by Foote 1966: 125) ♂ (WSU), USA: SOUTH DAKOTA [with labels with “S.D.,” “Type 100” (red writing), “*Euaresta tricolor* Doane” (handwriting, probably Doane’s, same as on label of wing slide (#31)), and red “Lectotype des. by Foote 1966 Proc. Ent. Soc. Wash. 68: 125 (Zack 1983)”]); Aldrich 1905: 613 [catalog].

Tephritis tricolor: Coquillett 1899: 264 [taxonomy].

Gymnocarena tricolor: Quisenberry 1950: 10 [taxonomy]; Foote 1960: 113 [taxonomy; Wisconsin], 1965: 676 [catalog]; Wasbauer 1972: 117 [host catalog]; Lisowski 1985: 111 [taxonomy; Indiana, Illinois].

Gymnocarena flava Foote, in Blanc and Foote 1987: 430 (Holotype ♀ (USNM), IOWA: Manson, Kalsow Prairie, 3.VIII.1973, W. B. Stoltzfus). **NEW SYNONYMY.**

[not] *Euaresta tricolor*: Huber 1927: 48 [misidentification of *Eutreta diana*].

[not] *Gymnocarena tricolor*: Grissell 1979: 753 [misidentification of *Eutreta diana*]; Blanc and Foote 1987: 429 [misidentification of *G. mississippiensis*].

Diagnosis.—*G. tricolor* differs from other *Gymnocarena* species except *G. mississippiensis* in having a bicolored yellow and brown wing pattern with 2 distinct light triangles in cells r_1 and r_{2+3} (see key to distinguish these two species). Only *G. diffusa* also has stout femora and all abdominal setulae yellow.

Description.—Setae and setulae yellowish. *Head*: genal height 0.36–0.45 times eye height; facial carina moderately to well developed, ventral expanded part large, its height $\frac{1}{3}$ – $\frac{1}{2}$ that of face, in lateral view, margin of ventral part straight to convex, more or less parallel with margin of facial ridge. *Thorax*: without small dark spots; mesonotum 2.62–3.09 mm long; dorsocentral setae more or less aligned with supra-alar setae. *Legs*: femora stout. *Wing* (Fig. 5H): pattern distinctly bicolored, dark brown from pterostigma and r-m to apex, at least basal third yellow; posterior half of r-m and all of dm-cu bordered by yellow; white areas are spots, not bands, including discreet spots in cells r_{2+3} (subbasal), br, and dm posterior to pterostigma; cell r_1 with 2 white marks, both extended into cell r_{2+3} apical to r-m, but neither extended beyond vein R_{4+5} ; cell r_{2+3} with extreme base yellow, with large subapical white spot not extended to margin; cell r_{4+5} with 2 large white spots in basal half, sometimes with small spot in apical half; cell m with 4 white spots. *Abdomen*: setulae on all terga yellowish. *Male terminalia*: outer surstylus with medium sized dorsal lobe; aedeagus 3.20–3.33 mm long, 1.04–1.18 times as long as mesonotum. *Female terminalia*: syntergosternite 7 1.46–1.58 mm long, 0.49–0.52 times as long as mesonotum; aculeus 1.37 mm long, tip (Fig. 8B) with sides nonserrate, moderately concave, extreme apex broad and blunt; 8th sternites

with apices at most slightly exposed in dorsal view, lateral margins evenly rounded.

Remarks.—Blanc and Foote (1987) misidentified as *G. tricolor* the species here described as *G. mississippiensis*. The species they called *G. flava* Foote is the true *G. tricolor*.

Huber (1927) reported that the types of *Callimome citripes* (currently *Torymus citripes* (Huber), Torymidae (Grissell 1979)) were reared from specimens of "*Euaresta tricolor* Doane on *Artemisia tridentata* Nuttall . . . recorded under Bureau of Entomology No. 3129." This record is an error, probably caused by confusion with the name *tricolor* Snow, a synonym of *Eutreta diana* (Osten Sacken). Two specimens in the USNM labeled with "3129" and dates matching those on card no. 3129 in the Bureau of Entomology file are *E. diana*, which is well known to breed in stem galls of *Artemisia tridentata* (Wasbauer 1972) and which has otherwise been reported as a host of *T. citripes* (Grissell 1979).

Biology.—W. B. Stoltzfus (pers. comm.) has reared this species from flowers of *Helianthus grosseserratus* M. Martens and *H. tuberosus* L. in Iowa.

Distribution.—(Map 1). South Dakota to Wisconsin and Indiana. I have not located the USNM specimen from Cranmoor [Wood Co.], Wisconsin reported by Foote (1960), but this locality is included on the distribution map. The square on South Dakota does not represent an exact locality; the specific type locality was not stated.

Specimens examined.—Lectotype of *tricolor*; holotype of *flava* (see synonymy). ILLINOIS: Boone Co.: 2.5 mi SW Cappon, 7.VIII.1980, E. A. Lisowski, 1 ♀ (INHS); Champaign Co.: Illini For. Plantation, 2.5 mi S Urbana, 21.VII.1979, E. A. Lisowski, 1 ♂ (INHS); DeKalb Co.: 1.5 mi E Fairdale, 7.VIII.1980, E. A. Lisowski, 1 ♂ (INHS); Livingston Co.: 2 mi W Fairbury, 22.VII.1980, E. A. Lisowski, 1 ♂ (INHS); McDunough Co.: 3 mi NE Bushnell, 29.VII.1980, E. A. Lisowski, 1 ♂ (INHS). INDIANA: Vermilion Co.: 0.5 mi N Eu-

gene, 15.VII.1980, E. A. Lisowski, 1 ♂ (INHS). "N. Amer.," 1 ♂ (BMNH). IOWA: Story Co.: Ames, 7.VII.1973, W. B. Stoltzfus, 1 ♂ paratype of *flava* (USNM).

ACKNOWLEDGMENTS

I sincerely thank the following individuals who arranged loans of material examined in this study: P. H. Arnaud, Jr. (CAS), D. Azuma (ANSP), F. L. Blanc (CDA), H. D. Blocker (KSU), G. W. Byers (UKaL), R. Contreras-Lichtenberg (NMW), J. M. Cumming (Biosystematics Research Centre, Ottawa) for loan of CNC material, D. Faulkner (SDNHM), R. L. Fischer (MSUEL), S. Frommer (UCR), J. K. Gelhaus (UKaL), D. A. Grimaldi (AMNH), W. J. Hanson (USU), V. Hernández (IEXV), J. Jenkins (MSUEL), D. Judd (AMNH), E. A. Lisowski (INHS), K. C. McGiffen (INHS), M. O'Brien (UMMZ), H. Schumann (ZMHU), S. R. Shaw (MCZ), G. W. Ulrich (UCB), H. V. Weems (FSCA), F. G. Werner (UAT), R. A. Wharton (TAMU), I. M. White (CAB International Institute of Entomology), N. P. Wyatt (BMNH), R. Zack (WSU).

A. Freidberg (Tel Aviv University), W. N. Mathis (Smithsonian Institution), J. Pakaluk and L. E. Carroll (Systematic Entomology Laboratory), and W. B. Stoltzfus (William Penn College) kindly reviewed the manuscript. The latter also very kindly allowed me to cite his unpublished host records for *G. diffusa* and *G. tricolor*. H. Robinson (Smithsonian Institution, Department of Botany) identified the *Dahlia* and *Verbesina* species. T. Griswald produced the illustrations of the wings and phylogenetic trees, and P. Malikul assisted with the SEM photographs.

LITERATURE CITED

- Aczél, M. L. 1950. Catalogo de la familia "Trypetidae" (Dipt. Acalypt.) de la region neotropical. *Acta Zoologica Lilloana* 7(1949): 177-328.
- . 1952. Suplemento al "Catalogo de la familia Trypetidae de la region neotropical." *Acta Zoologica Lilloana* 12(1951): 117-133.
- . 1954. Géneros y especies de la tribus "Trypetini." 3. Sobre los géneros *Rhagoletis*, "*Phorel-*

- lia," y *Tomoplagiodes*. (Diptera). *Dusenia* 5: 71-94.
- Aldrich, J. M. 1905. A catalog of North American Diptera. Smithsonian Miscellaneous Collections 46 (Publ. 1444). 680 pp.
- Beirne, B. P. 1971. Pest Insects of Annual Crop Plants in Canada, II. Diptera. *Memoirs of the Entomological Society of Canada* 78: 48-70.
- Bird, R. D. and A. V. Mitchener. 1954. Insects of the season 1953 in Manitoba, pp. 40-53. *In* MacNay, C. G., compiler, *The Canadian Insect Pest Review* 32: 1-129.
- Bird, R. D., D. R. Robertson, and A. G. Robinson. 1959. Manitoba, Insects of the season 1958, pp. 44-58. *In* MacNay, C. G., compiler, *The Canadian Insect Pest Review* 37: 1-122.
- Bird, R. D. and A. G. Robinson. 1956. Insects of the season 1955 in Manitoba, pp. 41-57. *In* MacNay, C. G., compiler, *The Canadian Insect Pest Review* 34: 1-138.
- Blanc, F. L. and R. H. Foote. 1987. Taxonomic observations on United States Tephritidae (Diptera), with descriptions of new species. *Proceedings of the Entomological Society of Washington* 89: 425-439.
- Byers, G. W., F. Blank, W. J. Hanson, D. F. Beneway, and R. W. Fredrickson. 1962. Catalogue of the types in the Snow Entomological Museum. Part III (Diptera). *University of Kansas Science Bulletin* 43: 131-181.
- Charlet, L. D., G. J. Brewer, and V. Beregovoy. 1989. Insect fauna of native *Helianthus* in southeastern North Dakota. *Proceedings Sunflower Research Workshop (National Sunflower Association)* 1989: 4-5.
- Coquillett, D. W. 1899. Notes and descriptions of Trypetidae. *Journal of the New York Entomological Society* 7: 259-268.
- Cresson, E. T., Jr. 1907. Some North American Diptera from the southwest. *Transactions of the American Entomological Society* 33: 99-108.
- Curran, C. H. 1934. *The Families and Genera of North American Diptera*. The Ballou Press, New York, N.Y. 512 pp.
- Doane, R. W. 1899. Notes on Trypetidae with descriptions of new species. *Journal of the New York Entomological Society* 7: 177-193.
- Dodson, G. 1987. Host-plant records and life history notes on New Mexico Tephritidae (Diptera). *Proceedings of the Entomological Society of Washington* 89: 607-615.
- Essig, E. O. 1926. *Insects of Western North America*. The Macmillan Co., New York, N.Y. 1035 pp.
- Farris, J. S. 1988. Hennig86 reference. Documentation for version 1.5. Stonybrook, N.Y.
- Fitzhugh, K. 1989. Cladistics in the fast lane. *Journal of the New York Entomological Society* 97: 234-241.
- Foote, R. H. 1960. Notes on some North American Tephritidae, with descriptions of two new genera and two new species (Diptera). *Proceedings of the Biological Society of Washington* 73: 107-118.
- . 1962. The types of North American Tephritidae in the Snow Museum, the University of Kansas (Diptera). *Journal of the Kansas Entomological Society* 35: 170-179.
- . 1965. Family Tephritidae (Trypetidae, Trupaneidae), pp. 658-678. *In* Stone, A., C. W. Sabrosky, W. W. Wirth, R. H. Foote, and J. R. Coulson, eds., *A Catalog of the Diptera of America North of Mexico*. United States Department of Agriculture, Agricultural Handbook No. 276.
- . 1966. Notes on the types of Tephritidae described by R. W. Doane. *Proceedings of the Entomological Society of Washington* 68: 120-126.
- . 1967. Family Tephritidae (Trypetidae, Trupaneidae). Fasc. 57. 91 pp. *In* Vanzolini, P. E. and N. Papavero, eds., *A Catalogue of the Diptera of the Americas South of the United States*. Departamento de Zoologia, Secretaria de Agricultura, São Paulo.
- . 1980. Fruit fly genera south of the United States. United States Department of Agriculture, Technical Bulletin No. 1600. 79 pp.
- Grissell, E. E. 1979. Family Torymidae, pp. 748-768. *In* Krombein, K. V., P. D. Hurd, Jr., D. R. Smith, and B. D. Burks, eds., *Catalog of Hymenoptera in America North of Mexico*, Vol. 1. Smithsonian Institution Press, Washington, D.C.
- Halfiter, G. 1987. Biogeography of the montane entomofauna of Mexico and Central America. *Annual Review of Entomology* 32: 95-114.
- Hering, E. M. 1940. Neue Arten und Gattungen. *Siruna Seva* 1: 1-16.
- Heiser, C. B., Jr., D. M. Smith, S. B. Clevenger, and W. C. Martin, Jr. 1969. The North American sunflowers. *Memoirs of the Torrey Botanical Club* 22: 1-218.
- Hendel, F. 1914. Die Bohrfliegen Südamerikas. *Abhandlungen und Berichte des Königlich Zoologischen und Anthropologisch-Ethnographischen Museums zu Dresden* 14(1912): 1-84.
- Hilgendorf, J. H. and R. D. Goeden. 1981. Phytophagous insects reported from cultivated and weedy varieties of the sunflower, *Helianthus annuus* L., in North America. *Bulletin of the Entomological Society of America* 27: 102-108.
- Huber, L. L. 1927. A taxonomic and ecological review of the North American chalcid-flies of the genus *Callimome*. *Proceedings of the United States National Museum* 70(2663): 1-114.
- Kamali, K. and J. T. Schulz. 1971. Rearing sunflower

- maggots, *Neotephritis finalis*, *Strauzia longipennis* and *Gymnocarena diffusa* (Diptera: Tephritidae) on artificial diets. Proceedings of the North Central Branch, Entomological Society of America 26: 85–86.
- . 1973. Characteristics of immature stages of *Gymnocarena diffusa* (Diptera: Tephritidae). Annals of the Entomological Society of America 66: 288–291.
- . 1974. Biology and ecology of *Gymnocarena diffusa* (Diptera: Tephritidae) on sunflower in North Dakota. Annals of the Entomological Society of America 67: 695–699.
- Knowlton, G. F. and F. C. Harmston. 1937. Utah Diptera. Proceedings of the Utah Academy of Science, Arts and Letters 14: 141–149.
- Lipp, W. V. and J. T. Schulz. 1970. Characterization and quantification of damage caused by selected species of sunflower feeding insects. Proceedings of the North Central Branch, Entomological Society of America 25: 27.
- Lisowski, E. A. 1985. Taxonomy and biology of *Strauzia* (Diptera: Tephritidae) in Illinois. Ph.D. dissertation, University of Illinois, Urbana-Champaign. 195 pp.
- Loew, H. 1862. Monographs of the Diptera of North America. Part I. Smithsonian Miscellaneous Collections 6 (Publ. 141). 221 pp.
- . 1873. Monographs of the Diptera of North America. Pt. III. Smithsonian Miscellaneous Collections 11 (Publ. 256). 351 pp.
- MacNay, C. G. 1952a. The Canadian Insect Pest Review 30: 121–147.
- . 1952b. The Canadian Insect Pest Review 30: 188–219.
- . 1952c. Summary of important insect infestations, occurrences, and damage in Canada in 1951. The Canadian Insect Pest Review 30: 297–341.
- . 1954. Summary of important insect infestations, occurrences, and damage in Canada in 1954. The Canadian Insect Pest Review 32: 342–389.
- . 1956. Summary of important insect infestations, occurrences, and damage in Canada in 1956. The Canadian Insect Pest Review 34: 303–337.
- McBride, D. K., D. D. Kopp, and C. Y. Oseto. 1985. Insect pest management for sunflower. North Dakota State University Extension Bulletin 28.
- McAlpine, J. F. 1981. Morphology and terminology—Adults, pp. 9–63. In McAlpine, J. F., et al., coords., Manual of Nearctic Diptera, vol. 1. Agriculture Canada, Monog. No. 27. Ottawa.
- Norrbom, A. L. 1987. A revision of the neotropical genus *Polionota* Wulp (Diptera: Tephritidae). Folia Entomologica Mexicana 73: 101–123.
- Norrbom, A. L. and K. C. Kim. 1988. Revision of the *schausi* group of *Anastrepha* Schiner (Diptera: Tephritidae), with a discussion of the terminology of the female terminalia in the Tephritoidea. Annals of the Entomological Society of America 81: 164–173.
- O'Grady, R. T. and G. B. Deets. 1987. Coding multistate characters, with special reference to the use of parasites as characters of their hosts. Systematic Zoology 36: 268–279.
- Papavero, N. 1971. Essays on the History of Neotropical Dipterology, with Special Reference to Collectors (1750–1905). Vol. I. Museu de Zoologia Universidade de São Paulo, São Paulo. 216 pp.
- Quisenberry, B. F. 1950. The genus *Euaresta* in the United States (Diptera: Tephritidae). Journal of the New York Entomological Society 58: 9–38.
- Snow, F. H. 1903. A preliminary list of the Diptera of Kansas. Kansas University Science Bulletin 2: 211–223.
- Snow, W. A. 1894. Descriptions of North American Trypetidae, with notes. Kansas University Quarterly 2: 159–174.
- Thomas, F. L. 1914. Three new species of Trypetidae from Colorado. The Canadian Entomologist 46: 425–429.
- Wasbauer, M. S. 1972. An annotated host catalog of the fruit flies of America north of Mexico (Diptera: Tephritidae). California Department of Agriculture, Bureau of Entomology, Occasional Papers No. 19: 1–172.
- Washburn, F. L. 1905. The Diptera of Minnesota. Minnesota Agricultural Experiment Station Bulletin 93: 19–168.
- Wiedemann, C. R. W. 1830. Aussereuropäische zweiflügelige Insekten, vol. 2. Hamm. 684 pp.

Note added in press. Two specimens were reared after acceptance of this paper: *G. mexicana*, MEXICO: MORELOS: Lagunas de Zempoala, emerged 1.VI.1992 ex. flowers of *Dahlia imperialis* (91M16) collected 23.IX.1991, A.L. Norrbom, 1♂ (USNM); *G. serrata*, MEXICO: MICHOACAN: road to Rincon de Curungo, 5 km NE of Zitacuaro, emerged 4.VI.1992 ex.

flowers of *Verbesina virgata* Cav. (91M35) collected 3.X.1991, A.L. Norrbom, 1♂ paratype (USNM). The larva of *G. serrata* left the capitulae to pupariate. Its puparium is very similar to that of *G. carinata*. The acronym IEXV, omitted from the list in Materials and Methods, represents the Institute de Ecología, Xalapa, Veracruz.